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AN ANIMAL CENSUS OF TWO PASTURES AND A MEADOW IN NORTHERN NEW YORK

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THE IMPORTANCE OF PASTURES AND MEADOWS IN NEW YORK STATE

About one-third of the area of New York State is covered with forest, and of the remainder, the farming area, nominally cultivated land, one-third is in pasture, one-third in meadow and the final third in plowed land. The most important crop raised in New York State is hay, and the one second in value is milk. But despite the fact that the hay comes from the meadows and that milk production is primarily dependent on pastures and meadows, and only secondarily on the cornfields and other cultivated crops, yet from the amount of attention that is paid to the pastures and meadows, one would think them of very minor importance. The farmer is primarily interested in his grasslands and in the amount of pasturage or hay they furnish to his live stock. What he sees in a pasture is a herd of cows and a few horses, little realizing that they represent an insignificant part of the total number of animals that are obtaining their nourishment there. Granting that most of the other animals are small, they make up in numbers what they lack in size. It is the purpose of this investigation to record a census of these animals in two pastures and one meadow, which, although possibly not typical of all pastures and meadows, will yet give some indication of the numerous population with which cows and horses share their food.

THE IMPORTANCE OF THE SMALLER ANIMALS

The economic aspect of the writer's investigations became apparent when it was found that where there were few cows in the pasture, the insects ate more of the grasses and clover than the cows did. And the cows succeeded in obtaining a larger share of the pasturage only when they kept the pasture so short that it offered scanty protection to the crickets, grasshoppers and leafhoppers, and was more attractive to the robins which foraged there in greater numbers and further reduced the numbers of insects. In the pastures examined, the grasses and clovers constituted only a third of the total vegetation, the other two-thirds being weeds, most of which the cows refused to eat. But the insects feeding on the weeds were only a third as numerous as those feeding on the grasses and clovers, and most of them were insignificant in size. The orchard grass and the red clover of the meadow were hosts for comparatively few insects, which, together with a single mowing, removed only a small part of the plant tissue produced. Thus the plant scavengers: millipedes, sowbugs, snails, and slugs, flourished in greatest abundance.

WHERE THE CENSUS WAS TAKEN

In the triangle formed by the junction of Steuben Creek and the West Canada Creek in Oneida County, New York, and south of the Trenton Falls—Frame's Corner road, is an area of about one square mile, the soil of which is almost entirely Merrimac Fine Sandy Loam (23).

The surface soil of the Merrimac fine sandy loam varies in depth from 6 to 10 inches and consists of a light-brown fine sandy loam. The subsoil to depths greater than 36 inches is a greyish-brown to light-brown loamy fine sand to fine sandy loam. The material throughout the soil section is loose and mellow. Some small gravel is encountered at depths varying from 10 to 15 feet. This soil is easily tilled, and can be cultivated under a wide range of moisture conditions. . . . The topography is level or nearly so, and the natural drainage is good.

The original forest growth on this type was chiefly pine, with hemlock, some hardwoods, and spruce. Where this timber was removed the land grew up in hemlock, maple and beech.

Some areas of this soil are adapted to early truck crops, such as cantaloupes and early potatoes, though the greater part of the type is suitable only to forestry.

A very small part of the Merrimac fine sandy loam is under cultivation. Corn yields 4 to 8 tons of ensilage per acre, oats 20 to 25 bushels, buckwheat 20 bushels, hay about 1 ton, and potatoes an average of 100 bushels. The methods of farming are generally poor. Little organic matter is returned to the land and only a few cattle are kept. . . . In general, this type is in need of organic matter, the addition of which renders it more resistant to drought.

The greater portion of this type is better suited to the growing of timber than to the production of cultivated crops. Much of it is forested with poplar and poor quality of hardwood. Some large areas have but little growth of any kind, and these could profitably be reforested. (pp. 46-48 of the "Soil Survey".)

This is not the typical soil type most common in the pastures of New York State, but on account of ease of access and availability, a meadow and two pastures in this area were chosen for making an animal census.

THE MEADOW

The meadow was the unwooded part of an old Methodist Camp Meeting Grounds and had been in continuous meadow for over fifty years, as it had never been plowed since the land was purchased by the Association in 1867. On the north side was woods, a second growth of maple, beech and basswood; on the east a pasture; to the south it was separated by two narrow gardens and a row of dying elms from an oat field; on the west was the wooded margin of Steuben Creek. In the middle of the meadow was a magnificent maple, and to one side a half-dead beech tree, the highest branches of which were the preferred perches of phoebes and kingbirds. The grass had been cut from the meadow every year, and the hay sold to the farmer

visitors to feed their horses, which were tied to a fence surrounding the grove where the meetings were held. Thus along the north edge of the meadow the ground was rather thoroughly manured each year by horse droppings. Despite the present popularity of the automobile, which has almost entirely eliminated the horses, the effect of their having been tied up to this board fence is still apparent in the vegetation, which sometimes consists almost entirely of orchard grass, while ten feet or more away from the fence, bluegrass, red clover and timothy are contesting for room with narrow-leaved plantain, sorrel and other weeds. In 1919, the hay was cut in the meadow on June 23d, but in previous years there had been a wide variation in the time of mowing, and ordinarily it had been so late that not only all the weeds, but also the red clover had a chance to seed, which in part explains its abundance.

THE PASTURES

The pasture at first selected was the one adjoining the meadow on the south, but it was found in practise that on days when there was a stiff wind from the south-east, no census could be taken in either pasture or meadow, and a pasture to the north of the woods, protected from the wind, was used. These two pastures were the day and night pastures of one farm.

The day pasture, which in this paper will be called the "Pasture of ABUNDANT Vegetation" (or sometimes abbreviated to "PAB" after dates) consisted of about 25 acres, a small part of which was in open woodland. It extended from the creek to the road, with woods on about half of both the other sides, but it was only in the open part between the woods that many observations were made.

The night pasture, called in the present discussion the "Pasture of SCANT Vegetation" (or sometimes abbreviated to "PSC" after dates) was only about 15 acres, and although not over-pastured, was used to the limit of its carrying capacity, as the cattle passed through it to reach the day pasture, to which they might not be transferred until 9:00 or 10:00 A.M., whenever the farmer happened to get back from the milk station.

Thus eight cows and one bull spent only 7 to 8 hours daily in the 25 acre pasture, while they were in the 15 acre pasture for the balance of the 24 hours, minus the time out for milking, or about 14 hours. Also, this pasture being adjacent to the barn, often had the horses turned out on it, with the result that the grass and even the weeds were very short indeed, while the grass in the night pasture was always longer, and weeds such as buttercups grew high. The average carrying capacity of the pastures of New York State is 32 cattle per 100 acres (41), and on this basis, there were 33 cattle per 100 acres in the pasture of scant vegetation, and 12 per 100 acres in the pasture of abundant vegetation. Both fields being of approximately the same natural fertility, their average carrying capacity, 22.5 cattle per 100

acres, is nearly a third less than that of the average for the state. If their position could be reversed, or the boundary fence changed, they should be able to furnish pasturage for four or five more cows. The farmer solved the problem a few years later by bringing part of the larger pasture under cultivation. About half of the pasture of scant vegetation was at a lower level and separated from the rest by a swale at the base of a rather steep slope, but observations were made only on the part at the same level with the meadow and the other pasture, so that so far as original soil conditions and elevation are concerned, all three fields are very much alike. Neither of the pastures had been plowed for at least 25 years and probably longer. Large areas of them were quite level and all of them sufficiently level so that they could be cultivated; merely they never had been as far back as the owner could remember.

Because of the abundance of weeds and the rather small number of cows per acre supported by the pastures, the conclusion should not at once be reached that the ineffective farming at present practised is due to intrinsically poor soil, but rather it seems to reflect the decreasing financial return for the present type of farming, primarily the comparatively low price paid for market milk. Ten or fifteen years ago, on the same farm from which the pastures were selected for investigation, they supported twice as many cows, and instead of one man alone trying to run the farm, it kept three (and during haying, four) men busy. Within a radius of two miles, the writer has seen five farmhouses become deserted and either fall down or be torn down, so that at present all that remains to mark their position is the falling-in foundation and the trees and shrubs grown wild that had been planted around the farm homes. Even more marked than the abandonment of the farm homes is the abandonment of the land itself for use in farming. In the triangle between the two creeks and the road, there are today only two bona fide farms, five of the others being occupied by city people who have built a golf course, tennis courts, lagoons, and planted young forest, and are playing with the more decorative aspects of farming by keeping sheep, ducks, geese and swans, or are merely doing nothing with the land by allowing it to grow up to grass, weeds and brush. The two other houses are occupied by the caretakers of the houses of the city people.

The two farms still being operated as farms did support large families on a scale of living which was generous by farming standards less than a generation ago, and while one farmer is making a good living, it is apparent that the other is barely making both ends meet. Yet neither of these farmers is doing as well, considering equipment used, time and money invested, and area farmed, as two families on the Camp Grounds, who on less than an acre each, are growing vegetables for local consumption and supplying the summer

needs of about one hundred people. As they have enthusiastically continued to garden on these areas for several years, it is evident that they are making a reasonable, and possibly a considerable, profit. The land on which these gardens are run is a slightly better portion of the permanent pasture and meadow on which observations were made in the present investigation.

It is not altogether certain that a more desirable or economic use for this type of soil than permanent grassland can be made without an entire change in the type of farming practised. And it is entirely outside of the province of this investigation to suggest such changes. But its results do suggest some modifications in the management of at least these pastures and this meadow, and they give a standard of comparison for similar investigations on the more usual Volusia Clay and Dunkirk Clay soil types which are more characteristic of the better permanent pastures and meadows of New York.

METHOD USED IN TAKING THE CENSUS

The method used in making the census was simple. A strong pail, thirteen and one-quarter inches in diameter, with handle attached to the bottom, and a hole with a screw cover in the center of the bottom, but with a sharp cutting edge around the top, made by the local tinsmith, was all the special apparatus needed. Armed with this pail, a large knife, forceps, hand-lens, ether, cyanide jar, newspapers and a large square of canvas, one was ready to begin operations. A circular area of one square foot, thirteen and one-quarter inches in diameter, having been selected from a distance of five or six feet away as being typical in flora of the meadow or pasture, the equipment, with the exception of the pail and knife, was put down. The pail was swiftly placed over the selected area with the weight of the investigator on top, to force the cutting edges of the pail through the vegetation and into the soil. The knife was used for cutting around the outside of the pail so that it would sink deeper into the soil, to a depth of three or four inches. Ether was then introduced through the hole in the bottom (now uppermost) of the inverted pail during a temporary removal of the screw cover. The vegetation for several inches around the pail was cleared away, so as to clearly mark the area when the pail was removed, and its removal and the writing of the preliminary notes usually took long enough for all the active animals under the pail to be anaesthetized. The pail could then be taken up without fear that any of them would escape. The square of canvas was spread out close to the circle of the area covered by the pail, and on hands and knees the investigator could grub up all the plants within the circle of the square foot and pick them to pieces, collecting every animal found into the cyanide jar. On the surface of the ground left exposed by the removal of the plants, animals could be seen and picked up as they began to move in reviving from the effects of the ether, but one always had to be careful to eliminate from the

count the active unanaesthetized animals running in from outside the foot circle, as the ants especially were apt to do.

The top two inches of earth is, in most cases, held together by a mat of interlacing roots, so that it can be dug up as a whole and flopped over on the newspapers, top down. By using care not to shake off too much dirt, all the small bits of dry grass and weed stems and other debris which covered the ground could be transferred to the paper, and when the mat of earth and roots was taken up, it was comparatively easy to distinguish and pick out all the live animals. Next, the mat of soil and roots is pulled to pieces over the papers, and finally all the soil dug up to a depth of foot, and everything in it noted.

By this method, most of the animals present were collected, certainly all those of appreciable size, but its accuracy was limited by the skill, care and patience of the operator. Ordinarly it took from one to two hours to collect and record the animals from one square foot. Eggs, especially when small and deposited in plant tissues are generally overlooked, and many small animals, especially nematodes in the soil, are not seen, and proper allowance should be made for the near-miscroscopic, non-motile forms of animal life which were not collected and are not here recorded. But, after a little practise and with reasonable care, practically every moving animal that could be seen with the naked eye was collected, and also all large eggs. Eggs of earthworms, slugs, spiders, crickets, grasshoppers, crambid and other moths, and of May beetles, all comparatively large forms, were found, but the eggs of the much more numerous but smaller leafhoppers and other small insects was not noted. In recording the data, an individual egg or a cluster of eggs are each credited as counting for one. The immature stages of all the animals, if unidentified at once, were either preserved, or an attempt made to rear to adult. In a few cases the preserved larvae could not be identified, even by those most competent to do so, but the most common cause of the numerous larval and pupal records without specific identification was death before transforming to adult.

ONE HUNDRED SQUARE FEET OF GRASSLAND WERE EXAMINED

It had been planned to take the census of one square foot every day, except when prevented by rain, from early spring to late fall, and, if possible, from snow to snow. There were three days of snowfall, April 24-26, after the first census of April 23, and it would have been possible to have made census examinations much earlier in the year, as during much of the exceptional winter of 1918-19 there was no snow on the ground. On the night of October 13, the day after the last census was taken, the ground froze solid

and remained frozen all day in the shade, but a few examinations could have been made after this date.

By the end of the season one hundred census examinations had been made, that is, all the animals from one hundred square feet had been recorded. It had been planned that one census should be made in the meadow and the next one in a pasture, but the final result was that fifty-one had been made in the meadow and forty-nine in the pastures, thirty-one in the pasture of scant vegetation and eighteen in the pasture of abundant vegetation.

THE SELECTION OF AREAS FOR EXAMINATION

The selection of the particular area for examination is a matter of considerable importance. The area should be typical of the environment or of some aspect of it. The amount of vegetation should be neither more nor less than the average, and if more one day, it should be less the next. A special effort, often made by persons when taking such a census for the first time, to include some particular plant or some noticeable large insect, is not to be entirely condemned, as the rest of the area and the remainder of the insects are quite likely to be average. In a few cases, particular areas were selected because they contained largely but one plant: moss on June 1, and July 4, and white clover on May 30; and although the number of animals found in the areas containing moss only was 15 and 16, and the one containing only white clover had 84, yet other areas in the same pasture selected only for their being typical contained as few as the moss area, and others many times as many as in the area of clover.

Also, if a sufficient number of examinations are made, the average, even of the widest extremes, is sure to give not far from a proper norm of the environment. The average of one hundred examinations, fairly evenly distributed from April to October, is unquestionably a correct picture, at least quantitatively, of the conditions in this permanent pasture-meadow area during the growing season. Even in the pasture of abundant vegetation, where only eighteen observations were made, no wide extremes were noted, and this number is sufficient for the average to be typical of the environment.

The importance of the selection of an average sample for investigation, or of making enough examinations to neutralize the abnormal samples and produce an average which will fairly represent the environment, should not be underestimated. Mr. McAtee (22) in a grassy meadow in March found 1,374 animals in four square feet, or 343 per square foot, but of this number, 933 were one species of ant, *Trematorium caespitum*, and "although there was no ant colony in the plot", yet for comparison with a woodland plot, he subtracts "these strongly contrasting elements", leaving 239 animals for four square feet, or 60 per square foot. This much more nearly approximates the results obtained in the present investigation, which totaled 6,843

TABLE 1. The Census of One Hundred Separate Square Feet of Grassland at Barneveld.

MEADOW

Date		Dominant Plant	Insects	Other Animals	Total Animals
April	23	Bluegrass	24	16	40
May	5	Sweet-scented grass	36	6	42
	13	Orchard grass	16	26	42
	16	Orchard grass	88	42	130
May	21	Orchard grass	5	27	32
	26	Red clover	41	6	47
	28	Narrow-leaved plantain	191	2	193
	29	Orchard grass	27	30	57
	31	Grass, plantain and sorrel	44	6	50
June	3	Dandelion	50	20	70
	4	Orchard grass	36	26	62
	5	Red clover	28	2	30
	7	Orchard grass	25	8	33
	11	Narrow-leaved plantain	49	2	51
	13	Orchard grass	39	12	51
June	17	Orchard grass	68	40	108
	20	Orchard grass	141	22	163
	23	Sweet-scented grass	53	2	55
	26	Orchard grass	27	13	40
	29	Strawberry plants	51	10	61
July	1	Orchard grass	30	7	37
	3	Red clover	76	17	93
	5	Red Clover	45	13	58
	8	Orchard grass	40	33	73
	12	Red clover	83	28	111
	14	Timothy and bluegrass	9	4	13
July	16	Red clover	67	3	70
	16	Orchard grass	42	15	57
	18	Strawberry plants	34	33	67
	22	Narrow-leaved plantain	25	15	40
	26	Orchard grass	40	42	82
August	4	Strawberry plants	67	32	99
	8	Narrow-leaved plantain	43	34	77
	11	Orchard grass	12	9	21
	13	Red clover	89	43	132
	15	Sweet-scented grass	19	3	22
August	20	Narrow-leaved plantain	48	58	106
	22	Strawberry plants	32	7	39
	24	Timothy	16	44	60
	30	Red clover	40	32	72
September	5	Red clover	32	19	51
	7	Red clover	46	32	78
	9	White clover	20	12	32
	11	Timothy	22	10	32
	13	Narrow-leaved plantain	22	31	53
	17	Red clover	29	20	49
	20	Red clover	32	32	64
September	30	Red clover	27	20	47
October	3	Bluegrass	23	29	52
	5	Orchard grass	19	31	50
	8	Timothy	21	10	31
		Totals	2189	1036	3225

PASTURE OF SCANT VEGETATION

Date		Dominant Plant	Insects	Other Animals	Total Animals
April	30	Dung and moss	50	20	70
	8	Bluets	34	6	40
	14	Everlasting and moss	121	8	129
May	19	Dung and white clover	17	19	36
	23	Dung and strawberries	96	17	113
	27	Dung and white clover	51	10	61
	30	Dung and white clover	79	5	84
June	1	Moss (*Polytrichum*)	14	1	15
	6	Redtop and low moss	57	2	59
	10	Dung and white clover	74	6	80
	14	Dung and chickweed	74	11	85
June	18	High buttercups	71	13	84
	24	Daisies and strawberries	50	1	51
	28	Redtop and *Veronica*	233	..	233
July	2	Dung and plantain	31	8	39
	4	Moss (*Polytrichum*)	10	6	16
	6	White clover and plantain	40	36	76
	13	Sweet-scented grass	10	5	15
July	17	Buttercup and clover	26	4	30
	23	Dung and sweet-scented grass	54	16	70
August	3	White clover	118	21	139
	9	Sweet-scented grass	43	7	50
	14	Sweet-scented grass	48	2	50
August	21	Bluegrass	73	4	77
	29	Dung and Canada thistles	28	15	43
September	6	Mint and white clover	82	5	87
	10	Bluegrass	24	20	44
	12	Bluegrass and low moss	39	12	51
	18	Dung and moss (*Polytrichum*)	21	8	29
October	4	Bluegrass and *Veronica*	48	9	57
	7	Dung and plantain	36	20	56
		Totals	1752	317	2069

PASTURE OF ABUNDANT VEGETATION

Date		Dominant Plant	Insects	Other Animals	Total Animals
May	15	Dung and white clover	37	41	78
May	20	Bluegrass	16	27	43
June	12	Bluegrass and buttercups	68	14	82
June	25	White clover	72	17	89
	30	High buttercups	127	16	143
July	9	Timothy and buttercups	112	12	124
July	15	Buttercups and timothy	117	5	122
	20	Dung and bluegrass	45	4	49
	25	White clover	82	17	99

Date	Dominant Plant	Insects	Other Animals	Total Animals
August 6	Timothy and plantain	102	56	158
12	Clover and low moss	99	9	108
August 16	Bluegrass	122	14	136
23	Narrow-leaved plantain	52	9	61
September 4	Bluegrass and sorrel	28	12	40
8	White clover and bluegrass	42	16	58
19	Buttercup and *Veronica*	26	9	35
October 1	Sweet-scented grass	36	17	53
12	Bluegrass and redtop	47	24	71
	Totals	1230	319	1549
	Total for 100 square feet	5171	1672	6843

animals for the 100 square feet examined, or, to compare with a locality where the climate more nearly approximates that of Washington, those of a previous investigation by the writer in central Illinois (39), where the animal population (counting grasshopper and mealybug egg-clusters as one, rather than each egg as a separate individual) averaged 57.5 per square foot in the fall and early winter, and 82.9 per square foot in the spring.

Mr. Morris (24) records finding 3,586,088 insects per acre, or 82 per square foot in a pasture in England. Dr. Beebe (4) found 250 living organisms per square foot of tropical jungle debris in Demerara, 65 per square foot of "leaves and moss from an uncleared area in the woods of a New York Zoological Park", and from tundra moss in Labrador, 3 organisms per square foot. The writer (41) collected 215 ants and 114 other insects and small animals from three square feet of pasture near the beach at Pt. Cangrejos, Porto Rico, or 110 animals per square foot.

Table 1 shows the amount of variation which occurs, even when every effort has been made to select typical samples, among insects and other invertebrates, and also the dominant plant in each square foot examined in the present investigation.

VEGETATION

In each square foot of the meadow and pastures examined, the plants were listed in what seemed to the observer to be the order of the amount in which they occurred (NOT the order of the number of plants of each species), or rather, in the order of the amount of animal forage they might furnish. Crediting each plant with ten points for first mention, nine points for second mention (second in abundance), eight points for third mention,—two points for ninth mention and one point for tenth, eleventh, twelth and thirteenth mention, their relative abundance has been determined, and is given in percentages of total vegetation in that environment, in Table 2.

The meadow and the pasture of abundant vegetation had several times as much total vegetation per unit of area as the pasture of scant vegetation,

TABLE 2. Relative Amount of Plants in Three Environments, Barneveld, New York.

MEADOW	Percent	Pasture of SCANT Vegetation	Percent	Pasture of ABUNDANT Vegetation	Percent
N. L. Plantain	14.5	White Clover	11.2	Bluegrass	12.9
Bluegrass	10.3	Bluegrass	9.6	N. L. Plantain	12.7
Orchard Grass	9.2	Moss	9.3	Buttercup	10.9
Red Clover	8.2	N. L. Plantain	8.5	White Clover	9.2
Timothy	7.7	Redtop	7.–	Violets	7.
Sorrel	7.7	Sorrel	6.9	Redtop	6.5
Daisy	6.7	Sweet-scented Grass	6.5	Veronica	6.
Buttercup	6.3	Daisy	5.9	Moss	4.7
Strawberry	6.–	Veronica	5.4	Strawberry	4.6
Violet	5.8	Violet	4.7	Timothy	3.7
White Clover	3.–	Buttercup	3.3	Sorrel	3.4
Sweet-scented Grass	3.–	Strawberry	3.3	Oxalis	3.
Dandelion	3.–	Canada Thistle	2.7	Blue Curl	2.7
Blue Curl	1.6	Oxalis	2.5	Everlasting	2.1
Oxalis	1.5	Chickweed	2.3	Dandelion	1.5
Yarrow	1.	Everlasting	2.	Sedge	1.4
Sedge	.6	Lichens (*Cladonia*)	1.4	Chickweed	1.2
Fern	.5	Blue Curl	1.3	Sweet-scented Grass	1.1
Lichens (*Cladonia*)	.4	Ironweed	1.	Jill over ground	1.1
Adder's Tongue	.4	Bluets	.7	Canada Thistle	1.
Everlasting	.3	Dandelion	.5	Adder's Tongue	.9
Veronica	.3	Adder's Tongue	.5	Daisy	.7
Hop Clover	.3	Yarrow	.5	Aster	.6
Dock	.3	Aster	.4	Lichens (*Cladonia*)	.5
Apple Tree	.3	Timothy	.4	Yarrow	.4
Cherry Tree	.2	Cornus	.4	Sweet Clover	.3
Maple Tree	.2	Sedge	.2	Ironweed	.2
Moss	.2	St. Johnswort	.2	Moth Mullein	.1
Plum Tree	.2	Alsike Clover	.1		
Devil's Paint Brush	.2	Foxtail Grass	.1		
Basswood Tree	.1				

and this is noted in connection with each animal which it affects. The point of vital interest to the farmer in this data is: how much of the vegetation is hay, and in the pasture, of value as forage for domestic animals. The plants of economic value have been separated from the others and listed together in Table 3.

In the list of economic plants of the meadow, only those which grow high enough to cut for hay are included, although white clover and sweet-scented grass, *Anthoxanthum odoratum*, are of decided importance in the pastures, even though the cows do not care much for the latter and leave it entirely where it is abundant.

John Burroughs (7) claims that the "narrow-leaved plantain is readily eaten by cattle and the honey bee gathers pollen from it," but it is doubtful if many farmers consider it anything but a weed. However, although it was only slightly less abundant in the pasture of abundant vegetation than in the meadow, there was considerably less of it in the pasture of scant vegetation, and apparently where other forage is scanty, the cattle eat it with sufficient

TABLE 3. Economic Plants in the Meadow and Pastures at Barneveld, N. Y.

MEADOW	Percent	Pasture of SCANT Vegetation	Percent	Pasture of ABUNDANT Vegetation	Percent
Blue grass	10.3	White Clover	11.2	Bluegrass	12.9
Orchard Grass	9.2	Bluegrass	9.6	White Clover	9.2
Red Clover	8.2	Redtop	7.–	Redtop	6.5
Timothy	7.7	Sweet-scented Grass	6.5	Timothy	3.7
Hop Clover	.3	Timothy	.4	Sweet-scented Grass	1.1
	35.7%	Alsike Clover	.1	Sweet Clover	.3
White Clover	3.	Foxtail Grass	.1		33.7%
Sweet-scented Grass	3.–		34.9%		
	41.7%				

relish to cause a marked decrease in its abundance. Many other weeds in the pasture are eaten by cows, more by accident than by design, but the feeding value of them is low, and they occupy land that might be growing more valuable plants.

From sixty-three to sixty-five percent of all vegetation in the three environments consists of plants of comparatively little or no value to the farmer: that is to say, these so-called grasslands are producing two-thirds weeds and one-third crop of grasses and clovers. This result is not due to the method of recording the data, as the method shows exactly what the farmer wants to know: the relative amount of vegetation available for animal food. If a different relative weight in points is credited to first, second, third mention, etc., this would not greatly affect the results obtained, as one weed, the narrow-leaved plantain, was more abundant than any one plant of economic value, and many of the weeds were more abundant in some environments than some plants of economic value.

AGRICULTURAL PRACTISES ENCOURAGE WEEDS IN GRASSLANDS

The reason why the economic plants occupy such a small place in the pastures and meadows is obvious. The farmer ordinarily cuts the grasses and clovers in the meadow just as they are about to mature seed, as that is the time when they are most valuable for hay, but the weeds, which mature seed at other times, both earlier and later, have this advantage in re-seeding themselves. Also, "as stock graze in the pasture, they select the plants they like and allow the undesirable kinds to grow and produce seed. This really is the cultivation of pasture weeds" (36). The farmer destroys the weeds which compete with his cultivated crops, but not only attempts no such aid for the grasses and clovers of his pastures and meadows, but rather cultivates the weeds.

Another factor, previously but little considered, is the animals other than the horses and cows, the wild animals which live in the meadow and pastures, and what effect these animals, especially the smaller ones, have in determining the comparative abundance of the weeds and the economic plants. As later will be shown in detail, the insects feeding on the economic plants are the largest in size and the greatest in number, while the weeds support an insignificant part of the insect population.

THE VERTEBRATES

Before proceeding to a detailed consideration of the smaller invertebrates, mention should be made of the vertebrates present, and how they affected the grasslands. The most obvious of course are the farmer's live stock, the cows and the horses, which supposedly disposed of more vegetation, left more manure, or rather left it in a more obvious form, and generally had more apparent effect than any other vertebrates. Of the wild vertebrates, in making an examination of only one square foot a day by the tin pail method, it was unlikely that any of them would be included. In the meadow near the gardens lived a solitary woodchuck, which, to judge from reports, foraged rather extensively in the gardens, but as it lived in the meadow, will be recorded as one woodchuck for ten acres of meadow. There were no fresh woodchuck holes in the pastures, probably because there was no red clover growing there, nor anything in the adjoining fields on which these animals could feed. In the woods, white-footed mice, chipmunks, squirrels and skunks were moderately abundant, but their excursions into the fields were infrequent or accidental, except possibly in the case of the skunks, and even they produced no appreciable effect.

Moles had made numerous tunnels in one part of the meadow where red clover was growing, and one might conclude that they had been feeding on the larger subterranean insect pests of this plant, especially the larvae and pupae of *Sitona* spp., and other epigeal Curculionids. But there was no indication of them in any other part of the meadow, nor in the pastures where these insects were also abundant. "From an examination of the stomach contents of 200 moles taken in all months of the year, it was found that earthworms and white grubs constitute the bulk of the food. Beetles and their larvae and other insects that enter the ground, spiders, centipedes, cocoons and puparia also form part of the diet. In one stomach were found the remains of 171 small white grubs, in another 250 ant puparia, in another 10 cutworms and in another 12 earthworms. Owing to their activity they sometimes consume each day a bulk of food equal to their own weight."(30)

No reptiles were noted in 1919, but from experience in years past, it is certain that ring-neck snakes, garter snakes, large black salamanders with bright yellow spots, and coral red ones with small black spots, were, or have

been, present. Any statistical method of discovering the abundance of these animals is lost between the gross method of counting the farmer's cows and of collecting the invertebrates under a foot square pail.

With the birds the situation is somewhat simpler and their abundance can at least be approximately estimated. The robin was by far the most common bird. Walking along the road between the pasture of scant vegetation and the woods late in the afternoon when the pasture was in the shade, as many as twenty robins have been counted which flew up out of the pasture into the woods. Of course not all of these robins were in the pasture all of the time, but making allowance for those not observed, a liberal estimate would give two robins per acre, at least for that part of the pasture between the swale and the woods, where all census examinations were made. In the meadow and in the other pasture, the robins were about half as abundant, probably because the grass was higher and did not approach the lawn-like condition of the scant pasture. Over half of the food of the robin consists of insects, and as they obtained a large portion of such food in the meadow and the pastures surrounding the woods where most of them nested, their effect, because of their size and abundance, on the insect life in that area was greater than that of any one or all the other birds present.

The only distinctively meadow bird present was a meadow lark, which lived in the oat-field adjoining the meadow and pasture on the south, and was only occasionally noted north of the fence. A pair of bluebirds built in the meadow fence, in a hollow post, and another pair lived in an old apple tree in the pasture of abundant vegetation in the corner most distant from the part where the census examinations were made. Several pairs of chipping sparrows lived in the edge of the woods by the meadow, but were seldom seen outside the protection of the trees, and then usually in the road. A pair of kingbirds lived along the fence between the two pastures, and another pair in the meadow, and one or another of a pair of phoebes spent most of the day along the fence or in a half-dead beech tree in the meadow, and every evening the male sang from the topmost bare branch. A pair of red-wing blackbirds nested in the swale in the pasture of scant vegetation, and sometimes there was quite a flock of them there. Several song sparrows and vesper sparrows also lived in or near the swale. Numbers of barn swallows had nests under the eaves of the nearest barn, but their feeding habits are so extensive that one bird for five acres is a liberal estimate. Three pairs of red-headed woodpeckers were twice seen on telephone poles in the pastures, but none nested nearby. A pair of flickers did their courting in a basswood tree beside the meadow, but apparently they built on the other side of the creek and little was seen of them during the summer. Crows and blue jays often flew by overhead without alighting, and there were occasional rare visitants, a scarlet tanager seen once, but when all records of all other birds than robins are put together, they scarcely equal half of this one bird.

TABLE 4. Summary of Vertebrates.

Animal	Meadow: 10 acres	Pasture of Scant eg tation: 15 acres	Pasture of Abundant Vegetation: 25 acres
Cows		1 per 3 acres	1 per 8 acres
Horses		2 occasionally	
Woodchuck	1		
Moles	many		
Robins	10	30	25
Meadow Larks	1	1	..
Bluebirds	2	..	2
Kingbirds	2	1	1
Phoebes	2	..	..
Song Sparrows	..	4	..
Vesper Sparrows	..	4	..
Red-wing Blackbirds	..	2	..
Barn Swallows	..	3	..
Total Birds	17	45	28

The total number of birds that can be definitely credited to the fifty acres of grassland as obtaining their food there is 90, or 1.8 birds per acre. Prof. Forbes (15) found that birds averaged 2.43 per acre of pasture and .74 per acre of meadow, late August to mid-October, but as the robin constituted only 2 percent of the native birds observed in Illinois, and the English sparrow, common only around farmhouses and barnyards at Barneveld, 34 percent of all birds, these data are hardly comparable.

THE INVERTEBRATES

In the following account of the invertebrates found, the primary aim, after noting the total number of individuals present in the hundred square feet of grassland examined, has been to indicate, and if possible explain, their relative abundance in the various environments, and how this affects the vegetation and the other animals occurring with them. Their feeding habits have been indicated when observed or known by the writer, or contributed by the specialist making the identification, or recorded in the literature which was available; but rather unfortunately in some cases, no special effort was made to observe the food, as it was taken for granted that no animal of numerical importance would occur in these environments unless there was something there for it to feed upon. This proved in general to be true, but several insects presumably not belonging to the grassland were found: two predaceous diving beetles several hundred yards from water, several Hemiptera ordinarily considered as feeding on vegetables, and on September 22, a moth of *Alabama argillacea* Hübner, the larva of which feeds only on cotton, considerable numbers of the moths being found a few days later.

No attempt was made at working out the life history of any of the animals, and such notes as are given are merely incidental, and are necessarily incomplete, especially of the less common species. However, the mass life history notes on some of the more common insects are possibly more accurate than more specific data on individuals observed under artificial conditions. For such data, and that on seasonal abundance, the investigation has sometimes been divided into ten periods each containing approximately ten examinations, roughly corresponding to half a month in most cases. These divisions are noted in Table 1.

THE DETAILS OF THE CENSUS OF THE INVERTEBRATES

Vermes NEMATODA

Twelve small nematodes were found, although this is merely the record of those large enough to be readily observed. The number would doubtless be largely increased if proper methods for separating them from their environment had been available.

Thirty-four hairworms, *Mermis* sp., were found, quite uniformly distributed in meadow and pasture. Eleven were in the top 2 inches of earth, 5 were 3 inches down, 6 were 4 inches down, 4 were 5 inches down, 6 were 6 inches down, 1 was 8 inches down, and 1 was at a depth of 12 inches, indicating a remarkable uniformity in abundance at all levels from the surface to six inches down, but few at greater depths. None of the grasshoppers or other large insects which serve as hosts for the hairworms was dissected.

Annelida CHAETOPODA

One hundred eleven earthworms were found in the 100 square feet, or slightly over one per square foot, or at the rate of 48,352 per acre. In a previous investigation in Illinois conducted by the writer from October to May (39), an average of 13.7 earthworms per square foot was found, or 596,772 per acre. The difference in season is partly responsible, as earthworms live at a lower level in the soil in summer, or else are really less abundant, but the difference is largely due to soil conditions, as the heavy clay soil of Champaign County, Illinois is an optimum environment for earthworms, while the Merrimac fine sandy loam, being deficient in humus and the property of holding moisture, is much less favorable.

It is interesting to note how the figures of the number of earthworms per acre found in these investigations compare with the data used by Charles Darwin (11). On page 160, he states:

> On the number of worms which live within a given space. . . . Hensen, who has published so full and interesting an account of the habits of worms (Zeitschrift für wissenschaft Zoolog., Vol. 28, p. 354, 1877) calculates, from the number which he found in a measured space, that there must exist 133,000

living worms in a hectare of land, or 53,767 in an acre. This latter number of worms would weigh 365 lbs., taking Hensen's standard of the weight of a single worm, namely one gram. It should be noted that this calculation is founded on the numbers found in a garden, and Hensen believes that worms here are twice as numerous as in corn fields. The above result, astonishing though it be, seems to me credible, judging by the number of worms which I have sometimes seen, and from the number daily destroyed by birds without the species being exterminated.

Fortunately for the accuracy of the main thesis of Darwin, on the rapidity and amount of the formation of vegetable mould, he did not use the number of earthworms given by Hensen, but measured the amount of mould directly. It seems scarcely possible that earthworms are only slightly less abundant in the none too fertile sandy pastures and meadow at Barneveld than in a European garden, while they are eleven times as abundant in the corn land of Illinois as in the garden. Yet, judging by a later statement of Darwin, the difficulty was not in there being too few worms to throw up the measured amount of mold, but too many. On page 175, he states:

How many live in old pastures is unknown, but if we assume half the above number (53,767), or 26,886 worms live on such land, then taking from the previous summary 15 tons as the weight of casting annually thrown up on an acre of land, each worm must annually eject 20 ounces. A full-sized casting at the mouth of a single burrow often exceeds, as we have seen, an ounce in weight; and it is probable that worms eject more than twenty full-sized castings during the year. If they annually eject more than 20 ounces, we may infer that the worms which live in an acre of pasture land must be less than 26,886 in number.

Four earthworm eggs were found May 21, and one in July 6, at Barneveld, and after mid-July, of all worms found, only two were small. In Illinois, earthworms just hatching were found March 20, and one egg on April 17. Earthworms were more abundant in the pastures than in the meadow, and considerably more abundant in the pasture of abundant vegetation. One fly, *Pollenia rudis* F., the larvae of which are parasitic on earthworms, was found Sept. 17m.

TABLE 5. Summary of Vermes and Annelida.

Total number collected	Number found in:			Number presumably present in 100 sq. ft. of:		
	51 sq. ft. of meadow	31 sq. ft. scant pasture	18 sq. ft. of abundant pasture	Meadow	Scant pasture	Abundant pasture
12 nematodes.....	8	4	0	16	13	0
34 *Mermis*.....	18	8	8	35	26	44
111 earthworms.....	47	34	30	92	110	166

Mollusca GASTROPODA

(All molluscs were determined, through the kindness of Dr. Paul Bartsch, by Dr. W. B. Marshall, of the U. S. National Museum.)

Eleven slugs, *Limax agrestis* L., and eleven eggs, probably of this species, were found, being considerably more abundant in the meadow. All of the eggs were found under a dense growth of orchard grass or bluegrass, eight on June 17 and three June 26. No slug was found between June 12 and August 30, although the first record is April 30 and the last Oct. 8, indicating that the summer is passed in the egg stage. Of the food habits of this species, Lovett and Black (21) state:

> They are practically omnivorous feeders, though showing a preference for a vegetable diet, they may often be found devouring small animal life, aphids, (sowbugs), earthworms, etc. They feed on decaying vegetation, putrid flesh, mushrooms, manure, etc. . . . They feed below, at the surface, or above the surface of the soil. In gardens and fields, practically all crops are attacked.

Fifty-nine of *Vallonia excentrica* Sterki, a small, flat (orbicular), white-shelled snail, were collected. Of these, 56 were in the meadow, and only 3 in the pasture. One of these (May 20pAB) was in the edge of the woods below the crest of the hill towards the creek, where the investigator had been forced to work by the too friendly advances of the bull, the other two (May 14pSC) were taken in an area containing mostly low everlasting and moss. Twenty-nine of those found in the meadow were in areas where orchard grass was dominant, and all the others where the vegetation was high, indicating a very decided preference by this snail for the moister environments.

Thirty-five of *Cochlicopa lubrica* Müll., a snail with a brownish opalescent, cornucopia-shaped shell, were noted, seven in the pasture close to the woods (May 20 pAB), the other twenty-eight in the meadow. Sixteen of the latter were in environments where orchard grass was abundant, two in unmowed meadow along the fence, six in high aftermath (Oct. 3 and 8), two where old leaves were abundant, and only one where the vegetation was scanty. The usual preference for the moister environments is marked.

Seven of *Zonitoides arboreus* Say, a snail with an opalescent flat shell, were collected May 21, Sept. 20, Oct. 3 and 8, all in meadow.

One of *Succinea* sp. was found June 17 in meadow.

One of the comparatively large *Polygyra monodon fraterna* Say was found Sept. 30 in meadow.

Of the total of one hundred twenty-five molluscs collected, one hundred ten were found in the meadow, and, in the great majority of cases, where the vegetation was long and dense, giving the desired amount of moisture (or protection from drying out), and an abundance of decaying vegetation for food.

TABLE 6. Summary of Mollusca.

Total number collected	Number found in:			Number presumably present in 100 sq. ft. of:		
	51 sq. ft. of meadow	31 sq. ft. of scant pasture	18 sq. ft. of abundant pasture	Meadow	pSC	pAB
22 *Limax agrestis*	17	2	3	34	6	16
59 *Vallonia excentrica*	56	2	1	109	6	5
35 *Cochlicopa lubrica*	28	..	7	55	..	38
7 *Zonitoides arboreus*	7	..	..	14	..	..
1 *Succinea* sp.	1	..	..	2	..	..
1 *Polygyra m. fraterna*	1	..	..	2	..	..
125	110	4	11	216	12	59

Arthropoda CRUSTACEA

One hundred twenty-three sowbugs, *Porcellio rathkei* Brandt., as determined by Miss Boone of the U. S. National Museum, were taken from the one hundred square feet of grassland, but of these, one hundred ten were from the meadow, and only thirteen from the pasture. Yet the most characteristic part of the pasture environment, the cow manure, is not objectionable, as four were found under dung, and all but two were in the same areas with dung. There appears to be no particular plant, or other factor in the meadow environment preferred by sowbugs, beyond a general preference for an abundance of vegetation. All except six were found above ground, and of the six, not one was below the humus-root area of the top two inches.

TABLE 7. Life History and Seasonal Abundance of *Porcellio rathkei*.

Period	Total collected	Comparative Size:			Proportion of adult to immature sowbugs
		Large	Medium	Small	
April-May	18	17	..	1	17
June	1	1	..	..	....
July	23	12	..	11	1.1
August	49	9	3	37	.225
September	19	6	9	4	.46
October	13	4	9	..	.44
TOTAL	123	49	21	53	

Table 7 shows their almost entire disappearance in June, followed by an abundance of immature stages, reaching a maximum in August.

In the Illinois investigations (39), sowbugs (possibly of a different species) were found much more abundant, averaging 1,260 per hundred square feet, being the most abundant animal, excepting only the earthworms which averaged 1,346 per hundred square feet, and more than making up for the millipedes, which have much the same food habits. The Illinois data are more nearly comparable to the meadow data of Barneveld, where

the sowbugs averaged 215 per hundred square feet. But even with the elimination of the pasture areas at Barneveld, the sowbugs are nearly six times as abundant in Illinois. In Illinois there was a rapid and steady increase in their numbers in the spring, so that in May (when the investigations were terminated) they were four times as numerous as during the fall.

MYRIAPODA

(All millipedes were identified by Prof. R. V. Chamberlin, University of Utah, Salt Lake City, Utah)

Eleven of *Polydesmus serratus* Say were taken in the hundred square feet, five in the meadow and six in the pastures. Those taken on June 12th, 13th and 17th were large, and the next records are of Oct. 4th and 12th, when both were small. These records would indicate the summer passed as eggs, hatching in the fall and becoming adult in June.

A total of six hundred twelve *Julus caeruleocinctus* Wood were found in the hundred square feet, the greatest number of individuals of any one species found during the investigation, not even exceeding any of the ants. Yet in proportion to the great abundance and comparatively large size of this animal, it has but slight influence on the living elements of its environment. "The mouthparts of millipedes are fitted for combing off decayed vegetable material, but not for attacking living plants." (Letter from Prof. Chamberlin.) The destruction of this decaying vegetable matter has comparatively little effect on the plants and other animals, and considering how many dead millipedes one finds, they can form only an insignificant factor in the food of birds.

They prefer environments of abundant vegetation, being only half as abundant in the pasture of scant vegetation. The greatest number found in any one square foot was 48. This was examined on August 6th in the pasture of abundant vegetation and contained 25 small millipedes on the surface of the ground, and 23 large ones three to six inches down in the earth, under an old cow dung. In the pasture of scant vegetation, the presence of dung in the area tripled the number of millipedes present, and in the other pasture multiplied their numbers by seven. The response of the millipedes was not only to the abundance of vegetation caused by the dung, but they also occurred in great abundance in the dung and probably fed on the particles of vegetation in it which had not been digested by the cows. The number of adults, as shown in Table 8, in proportion to the immature stages, is greatest in the latter part of May, from which time there is a constant decrease until the latter part of August, when the immature stages are three times as abundant as the adults, with a quick return by early October to the conditions of early spring.

Over half of the millipedes found, 322, were on or above the surface of the ground; over one-fourth, 183, in the top two inches of soil containing

TABLE 8. Life History and Seasonal Abundance of *Julus caeruleocinctus.*

Period	Number per square foot	Comparative Size:			Proportion of adults to immature stages
		Large	Medium	Small	
April-May	9.0	52	0	20	2.6
late May	4.0	31	7	2	3.5
early June	3.0	21	0	10	2.1
late June	5.6	35	3	18	1.7
early June	5.0	23	16	16	.72
late July	5.6	26	18	12	.86
early August	9.2	35	25	32	.61
late August	9.5	20	19	37	.35
September	7.–	54	10	29	1.64
early October	5.0	30	7	4	3.33
	...	327	105	180	....

most of the plant roots, but slightly over one-sixth, 107, were below the top two inches, some being as much as six or eight inches down. Four-fifths of those found at the lower levels were there during midsummer.

In Illinois the millipeds averaged only 174 per hundred square feet, but their place as scavengers of decaying vegetation was more than made up for there by the large number of sowbugs.

TABLE 9. Summary of Crustacea and Myriapoda.

Number Collected	Number found in:			Number presumably found in 100 sq. ft. of:		
	Meadow	pSC	pAB	Meadow	pSC	pAB
123 *Porcellio rathkei*	110	3	10	215	10	55
612 *Julus caeruleocinctus*	389	106	117	762	342	650
11 *Polydesmus serratus*	5	3	3	10	10	16

Arachnida ARANEIDA

(All spiders, unless otherwise noted, were determined by Prof C. R. Crosby, of Cornell University.)

Four hundred seventy spiders were found in the hundred square feet of grassland, being considerably more abundant in the environments of abundant vegetation.

Four specimens of *Asagena americana* were found in the pasture of scant vegetation; 3 on May 23d, 1 on Oct. 7th, but this was the only spider showing a preference for the environment of scant vegetation.

The Erigonid spiders, which constituted over half of all collected, showed a very decided preference for the environments of abundant vegetation, being nearly twice as abundant (247 per hundred square feet) in the pasture of abundant vegetation as in the other pasture (145 per hundred square feet), and nearly three times as abundant (362 per hundred square feet) in the meadow. *Erigone autumnalis* Emerton, a very small, light-colored spider

with a yellow head, was most abundant in the pasture of abundant vegetation, and was rather scarce in the meadow, but the others, *Caracladus gigas*,[1] *Ceraticelus emertoni*, and *C. micropalpis*, *Ceratinella brunnea*, *Porosopotheca* spp., *Grammonota ornata* and *G. inornata*, were very abundant in the meadow.

A few individuals of *Linyphia pusilla* were found, and some that were possibly *Tetragnatha* sp.

Eight individuals of *Argiope trifasciata*, a large brilliant black and yellow spider with a silvery thorax, and one of *A. aurantia*, were noted between mid-June and mid-September.

Fifteen spiders of *Araena*, or allied genera, were collected, two of *Marxia stellata*, and as tentatively determined by the writer, one of *Leoscona benjamina*, one of *Araena thaddeus*, and two of *Araena pegnia*.

One *Misumena aleatoria* (*asperata* Hentz.) was collected Sept. 8th in the pasture of abundant vegetation.

Twenty-nine spiders of the genus *Xysticus* were found, over three times as abundant in the pasture of abundant vegetation as in the other environments. As determined by the writer, nine were *Xysticus ferox*, four *X. triguttatus*, one *X. formosus*, one *X. nervosus*, and the others unidentified as to species. Fourteen spiders of the genus *Lycosa* were collected, but none identified as to species.

Pirata minutus was one of the more abundant spiders, being found from early spring to late fall, and most readily distinguished by the silvery spots on the side of the abdomen. A total of 83 individuals was noted, with 11 egg-clusters. The first female carrying eggs was noted on June 18th, the last on July 23d. Females carrying egg-masses were four times as abundant in the pasture of scant vegetation as in the other environments, although at other times they occurred with equal abundance in the other environments.

Eight individuals of a small dark brown Attid spider with noticeable bright yellow mandibles and yellow and brown legs, were found, being three times as abundant in the meadow as in the pastures. One large Attid, *Evarcha hoyi*, was taken July 16th in the meadow, and one of *Salticus scenicus* July 23d in the scanty pasture.

ACARINA

(All determinations of mites were by Dr. H. E. Ewing, of the U. S. Department of Agriculture, Bureau of Entomology.)

A total of one hundred seventy-four mites, probably all belonging to the families Erythraeidae, Trombidiidae and Gamasidae, were found in the hundred square feet. The bright red ones, ninety-eight in number, some of which were identified as *Allothrombium pulvinus*, *A.* sp., *Atomus* sp. and

[1] "There is some doubt as to the determination of this species, as the specimens are all females. I have sent them to Mr. Emerton, and he thinks that they are *C. gigas*, but I have compared them with the only specimen I have, taken at Lake Tear on Mount Marcy, and still have some doubts as to their being the same." (Letter from Prof. Crosby.)

TABLE 10. Summary of Araneida.

Total number collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
4 *Asagena americana*	..	4	..	..	13	..
46 *Caracladus gigas*	34	9	3	67	29	16
62 *Ceraticelus* spp. & *Ceratinella brunnea*	38	10	14	75	32	78
102 *Prosopotheca* spp. & *Grammonota ornata*	71	14	17	139	45	93
43 *Grammonota inornata*	36	6	1	71	20	5
29 *Erigone autumnalis*	7	10	12	10	19	55
3 *Linyphia pusila*	..	1	2	..	3	10
3 *Tetragnatha?*	2	1	..	4	3	..
9 *Argiope* spp.	7	2	..	13	6	..
15 *Araena* spp.	9	2	4	17	6	16
1 *Misumena aleatoria*	..	..	1	..	..	5
29 *Xysticus* spp.	11	6	12	21	20	66
14 *Lycosa* spp.	7	3	4	14	9	22
94 *Pirata minutus*	43	33	18	84	106	100
10 Attid spiders	7	3	..	14	10	..
6 Egg-masses	..	3	3	..	9	16
470 Spiders & egg-masses	272	107	91	529	330	482

Microtrombidium magnitarsae, were most common in the environments of abundant vegetation. The first adult females were found on April 23, became quite abundant in late May, but none was noted from early June to September. Larvae were present throughout the season, being most abundant in May and September, over a fourth of them being attached to hosts.

Eight were found on both the nymphs and adults of the large green leafhopper, *Dracculacephala mollipes minor* Walker, and they were noted on many more of these leafhoppers than came within the limits of the areas being examined. Two large red mites, Erythraeid larvae, almost as large as the host, *Agallia 4-punctata* Provancher, and seven more Erythraeid larvae were found on the tree-hoppers, *Entylia carinata* Forst., which live on everlasting. One mite was found on a Syrphid fly, *Mesogramma marginata* Say. These mites are true parasites and often kill their small hosts. The unattached immature mites were not found below the surface of the ground, but one large female was about two inches down (April 30), and two others were found under cow dung (May 15). Eight black mites with red legs were found in the pasture, May 8 and 15.

Sixty-eight yellowish or brownish mites were found, some of which were identified as Gamasid nymphs. Two were on the beetle, *Hister americanus* Payk., one on *Aphodius fimetarius* L., four on *Onthophagus hecate* Panz., all dung-feeders or scavengers, but one was found on the back of the clover leaf weevil, *Sitona hispidula* F. All the others were unattached to hosts.

Dr. Banks (3) says of the Gamasids (Parasitus): "They are always predaceous and are sometimes beneficial in destroying springtails and injurious mites." Dr. Ewing in a letter to the writer, notes that: "some species are true parasites, many are commensals, and some attach to other arthropods for purposes of transportation only."

TABLE 11. Summary of Acarina.

Total Number Collected	Number found in:			Number in 100 sq. ft of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
106 *Erythraeidae*	52	12	42	101	39	232
68 *Gamasidae*	25	36	7	49	116	39
174 mites	77	48	49	160	155	271

INSECTA

COLLEMBOLA, OF SPRINGTAILS

Ninety-three springtails, identified by Prof. J. W. Folsom, of the University of Illinois, as *Tomocerus flavescens* Tullberg, of two varieties; *americanus* Schott, and *separatus* Folsom, were found in the hundred square feet. Their numbers were almost equally divided in the various environments, but they were considerably more abundant in early spring, midsummer (early July) and late fall than in the late spring and late summer. Prof. Folsom writes of this species, in a letter to the writer:

"*Tomocerus flavescens* is a common species throughout Europe, and in this country we have three varieties of it, but not the typical form. It occurs in humus or among dead leaves on damp soil, or under logs and stones. It does not occur on green plants, but I have kept it alive for months on pieces of moist decaying wood. It feeds on particles of decaying organic matter and fungi. . . . Three kinds of fungus spores were found repeatedly in different specimens, often in such quantity as to nearly fill the digestive cavity. These were *Capnodium salicinum, Macrosporium* and *Trisporium,* as determined by J. T. Barrett of the University of Illinois. There were often gregarine parasites in the mid-intestine, also."

EUPLEXOPTERA, OR EARWIGS

One very small earwig, probably *Labia minor* L., was found July 13th in the pasture of scant vegetation.

ORTHOPTERA

(All Orthoptera were determined by Mr. N. A. Caudell, of the U. S. National Museum.)

Sixty-seven grasshoppers, one katydid and one cluster of five grasshopper eggs were found in the hundred square feet. The grasshoppers were

twice as abundant in the pasture of abundant vegetation as in the meadow, and over twice as abundant in the meadow as in the pasture of scant vegetation. The cluster of five eggs was found Sept. 11th, in the meadow.

TABLE 12. Summary of Orthoptera.

Total Number Collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
13 *Tettigidea lateralis* var. *polymorpha* Burm.	5	3	5	10	10	27
5 *Orphulella speciosa* Scudd.	..	..	5	..	..	27
11 *Stenobothrus curtipennis* Harris	6	1	4	12	3	22
1 *Encoptologhus sordidus* Burm.			1			5
2 *Hippiscus* nymphs	..	1	1	..	3	5
16 *Melanoplus femur-rubrum* DeGeer	10	2	4	19	6	22
3 *Melanoplus femoratus* Burm.	2	..	1	4	..	5
1 *Scudderia furcata* Burm.	1	..	..	2	..	..
16 *Conocephalus brevipenne* Scudder	8	2	6	16	6	33
1 egg-cluster	1	..	..	2	..	..
69 grasshoppers	33	9	27	67	32	146
46 *Grillus assimilis* F.	16	8	22	31	26	117
81 *Nemobius fasciatus* DeGeer	20	15	46	39	48	255
127 crickets	36	23	68	70	74	372

No nymphs of *Melanoplus femoratus* were found, nor adults of *Hippiscus* sp., so it is quite possible that adults of the latter migrated elsewhere, and that those of the large *Melanoplus* migrated here from other fields. The very rapid growth and development of the small nymphs, first noted in early summer, to fully-grown nymphs and then adults by midsummer was most interesting to watch. Both nymphs of *Hippiscus* were quite large and were found May 5th and 15th, before those of any other species had been seen. Of several species also, the smallest nymphs happened not to come within the limits of the areas examined, but the nymphs of *Melanoplus femur-rubrum* found on May 29th were very small and had hatched only a short time before, as was also true of the first record of *Conocephalus brevipenne*, June 11th, and of *Orphulella speciosa* June 20th. A very small nymph of *Tettigidea lateralis* was found July 9th, but large nymphs had been taken two weeks before. The first records of the adults are: July 14, *Melanoplus femoratus;* July 20, *Orphulella speciosa;* July 25, *Stenobothrus curtipennis;* Aug. 6, *Tettigidea lateralis,* and *Conocephalus brevipenne;* Aug. 12, *Melanoplus femur-rubrum.*

One hundred twenty-seven individuals of two species of crickets were found in the hundred square feet: forty-six of *Grillus assimilis* F., the larger species, and eighty-one of *Nemobius fasciatus* var. *vittatus* Harris, a smaller cricket. They showed a striking preference for the pasture of abundant vegetation, where they were five times as abundant as in the other environ-

ments. This is possibly a response to the cumulative effects of the abundant vegetation, the dung and the one-third greater abundance of all animals in this pasture. So far as food is concerned, crickets seem admirably adapted to thrive anywhere, as they were observed to eat injured crickets, millipedes and earthworms not yet dead, grass, bread crumbs, moist newspaper, and occasionally took a nip of the writer. On September 19th, large numbers of both species collected on the canvas, newspapers and in the hole where the examination was being made. Possibly the freshly exposed earth was attractive to the females seeking to oviposit. Eggs were found May 15th and 16th, the first nymphs early in June, the adults of both species late in August, and females ovipositing on Sept. 19th. From mid-June, when small nymphs were abundant, there was a steady decrease in abundance of both species, their numbers decreasing as the individuals increased in size.

THYSANOPTERA

Seventy-four thrips, identified by Mr. A. C. Morgan, of the Clarksville, Tenn. laboratory of the Bureau of Entomology, as *Haplothrips graminis* Hood, were found in ten daisy flowers, June 11th to July 6th, twenty-eight being on one flower, and two flowers having none.

HEMIPTERA

(Unless otherwise noted, all bugs were determined by Miss E. Wells, formerly of the U. S. National Museum.)

Reduviidae

One adult of the predaceous *Sinea diadema* F. was found September 30th in the meadow.

Nabidae

Five individuals of *Nabis* (*Coriscus*) *ferus* L. were found, mostly during the month of August, and ten of *Nabis subcoleopteratus* Kirby from late June to early August. Both species are predaceous.

Aradidae

Six adults of *Acalypha lillianis* Bueno were found in the pasture of scant vegetation, May 23d to June 24th. Mr. H. S. Barber states that these insects feed on moss.

Miridae (*Capsidae*)

Twenty-eight Capsids were found during the summer, thirteen of which were *Miris dolobratus* L. Nymphs of this species were first noted June 12th, and the last adult of Sept. 30th. This insect feeds on grass, especially timothy (29), and it was several times as abundant in the environments of abundant vegetation. Prof. Osborn discusses *Reduviolus* (*Nabis*) *ferus* as predaceous on this insect, but it seems probably that most of the food of

these predaceous bugs would consist of leafhoppers, which are nearly seventy times as abundant.

The other Capsids were: three adults of *Lygus praetensis* L., five adults of *Halticus citri* Ashmead, two of *Collaria occulata* Reuter, one of *Poecilos-cytus basalis* Reuter (det. W. L. McAtee), one nymph of *Psylla annulata* Fitch (det. W. L. McAtee), and three undetermined nymphs.

Lygaeidae

One adult of *Cymus angustatus* Stal, the false chinch bug, a general feeder on many cultivated plants, was taken Sept. 17th in the meadow. Forty-nine individuals, twenty-five nymphs and twenty-four adults, of *Geocoris uliginosus* var. *limbatus* Stal were taken in the hundred square feet, or on an average of one to two square feet. They were more than twice as abundant in the meadow as in the pastures. They are supposed to be omnivorous, but their feeding habits were not observed. Although rather small, because of the abundance of this insect and its probable predaceous habits, it is worthy of more attention than it appears to have received from economic workers. Judging by Table 13, there are two generations during the summer.

TABLE 13. Seasonal Abundance and Life History of *Geocoris uliginosus limbatus.*

Period	Nymphs	Adults
May 13	1	..
late May	9	..
early June	9	1
late June	..	3
early July	..	1
late July	2	5
early August	3	7
late August	1	..
September	..	5
October 5	..	2
Totals	25	24

Coreidae

One adult of *Alydus eurinus* Say, which is supposed to be mainly predaceous, was collected October 5th in the meadow.

Pentatomidae

One adult of *Coenus delius* Say was collected August 22nd in the meadow, and two nymphs on June 24th and July 5th. One adult of *Euschistus variolarius* P.B. was found May 26th in the meadow, and eleven nymphs of what was probably this species were collected through the summer. These insects are said to be omnivorous, but are mainly plant feeders.

Corimelaenidae

Five individuals of *Thyreocoris ater* A. & S., as determined by Mr. E. H. Gibson, were found June 29th to August 22nd, four of them being in the meadow. This insect is said to be herbivorous.

TABLE 14. Summary of Hemiptera.

Total Number Collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
1 *Sinea diadema* F.	1	..	..	2	..	..
5 *Nabis ferus* L.	1	4	..	2	13	..
10 *N. subcoleopteratus*	2	3	5	4	10	27
6 *Acalypha lillianis*	..	6	..	..	16	..
13 *Miris dolobratus* L.	8	2	3	16	6	22
3 *Lygus praetensis* L.	1	2	..	2	6	..
5 *Halticus citri* Ashm.	4	1	..	8	3	..
2 *Collaria occulata* Reut.	..	2	..	..	6	..
1 *Poeciloscytus basalis*	..	1	..	..	3	..
1 *Psylla annulata* Fitch	..	..	1	..	..	6
3 Capsid nymphs	3	..	..	6	..	..
1 *Cymus angustatus* Stal.	1	..	..	2	..	..
49 *Geocoris u. limbatus*	33	11	5	64	35	27
1 *Alydus eurinus* Say	1	..	..	2	..	..
3 *Coenus delius* Say	2	1	..	4	3	..
12 *Euschistus variolarius*	4	6	2	8	18	11
5 *Thyrecoris ater* A. and S.	4	..	1	8	..	5
121 bugs	65	39	17	128	121	97

Of the 121 Hemiptera, 66 are predaceous wholly or in large part, and 55 are phytophagous.

HOMOPTERA

Fulgoridae

Nineteen Fulgorids were collected during the summer. Two adults of *Bruchomorpha oculata* Newman were found Aug. 13th and Sept. 5th in the meadow, and twelve of what were possibly nymphs of this species, black with a few white spots, were found from June 12th to July 23d, but almost entirely in the pastures.

Four plump grey nymphs were collected between Aug. 15th and October 8th, but no adults to which they could be assigned. One slender yellow nymph was found Sept. 5th in the meadow.

Cercopidae

Sixty-one froghoppers were found in the hundred square feet: 24 *Philaenus lineatus* L., the grass-feeding froghopper, 35 *Philaenus spumarius* L., the meadow froghopper, 1 *Lepryonia gibbosa* Ball and 1 *Clastospera obtusa* Say. (Miss Wells identified some of the specimens of *P. spumarius* as *P. leucophthalmus* L. and *P. leucocephalus* L.) In the pasture of abundant vegetation, the two common froghoppers were of equal abundance, but *P. lineatus* was most abundant in the pasture of scant vegetation, and *P. spumarius* very considerably more abundant in the meadow, yet their respective food-plants, as given by Prof. Osborn (28), grass for the former and weeds and clover for the latter show no such variation in the different environments. He further states that timothy and redtop are the preferred food-plants of *P. lineatus*, but all nymphs noted at Barneveld were on blue-grass. Eleven of the nymphs of *P. spumarius* were feeding on daisy, five on buttercup, three on narrow-leaved plantain, three on devil's paintbrush, one on white clover and one was on the ground. As will be noted in Table 15, the nymphs of both species were first noted during the latter part of May, were abundant and noticeable during June, the last nymph of *P. spumarius* being found on June 17th, that of *P. lineatus* on June 24th. The first adults were noted on June 26th and 29th, and occasional adults were collected throughout the summer up to the date on which the final examination was made, October 12th.

TABLE 15. Life History and Seasonal Abundance of Two Froghoppers.

Period	*Philaenus spumarius*		*Philaenus lineatus*	
	Nymphs	Adults	Nymphs	Adults
late May	2	..	4	..
early June	15	..	2	..
late June	9	1	4	3
July	..	2	..	1
August	..	5	..	6
September	..	..	..	..
October	..	1	..	4
	26	9	10	14

The single adult of *Clastospera obtusa* Say was collected October 7th in the pasture of scant vegetation. The nymphs of this froghopper are recorded by Osborn (28) as feeding on alder, white birch and hazel in Maine, but the latter two do not occur in this part of New York State, and the nearest black alders growing along the bank of Steuben Creek are several hundred yards distant.

The single adult of *Lepryonia gibbosa* Ball was collected Sept. 30th in the meadow.

Membracidae

Three adults of the tree-hopper, *Stictocephala lutea* Walker, were found in the meadow on red clover from May 26th to July 3d. Two nymphs were collected: one on April 30th in the pasture of scant vegetation, the other on September 30th in the meadow.

Eight adults of *Entylia carinata* Forster (=*bactriana* Germar) were on everlasting, September 8th in the pasture of abundant vegetation, with one to three red mites (Erythraeid larvae) on several of them.

Two adults of *Campylenchis latipes* Say were noted on Canada thistle, August 12th in the pasture of abundant vegetation.

Ten unidentified nymphs, tentatively identified by Mr. W. L. McAtee as *Ceresa* sp., were found from August 13th to September 20th in the meadow, and three were found in the pasture of abundant vegetation on June 12th. All have two rows of branching spines running along the back, considerably separated at the head, but close together on the thorax and abdomen, and with a single caudal branched spine. There are three pairs of spines on the head, two pairs on the thorax and five pairs and the caudal spine on the abdomen.

TABLE 16. Summary of Fulgoridae, Cercopidae and Membracidae.

Total Number collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
19 Fulgoridae	7	6	6	12	20	32
24 *Philaenus lineatus*	8	12	4	16	38	22
35 *Philaenus spumarius*	26	5	4	51	16	22
2 other Cercopidae	1	1	..	2	3	..
61 froghoppers	35	18	8	69	57	44
6 *Stictocephala lutea*	4	2	..	8	6	..
8 *Entylia carinata*	..	..	8	..	..	44
2 *Campylenchis latipes*	..	..	2	..	..	11
13 *Ceresa* sp.	10	..	3	19	..	16
29 treehoppers	14	2	13	27	6	71

Cicadellidae (Jassidae)

(Unless otherwise noted, all leafhoppers were identified by the writer.)

One hundred one individuals of the clover leafhopper, *Agallia 4-punctata* Provancher, were collected in the hundred square feet, being considerably more abundant in the pasture of scanty vegetation where white clover, the usual host, is most abundant.

As shown in Table 17, there are two generations of this leafhopper during the year. The first small nymphs were noted on May 6th, the last large nymphs of the spring generation July 3d, and the last adult July 12th. The

TABLE 17. Seasonal Abundance and Life History of *Agallia 4-punctata.*

Period	Small Nymphs	Large Nymphs	Adults
late April	..	3	..
early May	6	..	..
late May	10	4	5
early June	..	19	6
late June	..	9	4
early July	..	1	9
late July	10	..	..
early August	2	..	..
late August	3	1	..
September	..	6	1
October	..	2	..
	31	45	25

first nymphs of the summer brood were seen on July 23d, and the only adult of this generation on September 8th. Some of the nymphs of this brood undoubtedly hibernate, as the last one found in the fall, on October 8th, and the first in the spring, April 23d and 30th, were large. A nymph collected on August 24th in the meadow had two red mites (Erythraeid larvae) on it, which were almost as large as the leafhopper itself.

Sixteen individuals of *Kolla bifida* Say were collected, the first very small chalky white nymphs on June 26th, larger nymphs on July 22nd, the first adults three days later, and the last adult on August 11th. All the individuals, except one adult, were found in the meadow, and in areas where orchard grass was most abundant, although usually bluegrass and timothy were present. Prof. Osborn (26) gives bluegrass as its special host-plant, and states that "it has been collected in rank bluegrass in such numbers as to give an estimate of 50,000 per acre." During the period when *Kolla bifida* occurred, sixteen square feet of meadow were examined, from which fourteen individuals were collected, which gives an abundance of 38,115 per acre, and this for one of the least abundant leafhoppers.

Thirty-two individuals of *Draeculacephala mollipes minor* Walker, as determined by Miss Wells, were collected in the hundred square feet, 25 of them in the meadow, especially from the high orchard grass, bluegrass and timothy. Nymphs were noted from May 16th to 29th, adults from May 29th to July 9th; nymphs of the second generation from August 20th to October 5th, and adults of this generation from September 11th to October 8th. Five nymphs and three adults had red mites on them, and this leafhopper was a favorite host of the mites, more being noted on this one, swift-moving species than on all other insects.

Four hundred ninety-nine individuals of *Acucephalus striatus* L. (or *Stroggylocephalus agrestis* Fallen, as Miss Wells identified them) were collected in the hundred square feet, or 217,364 per acre, constituting nearly half of all leafhoppers found. They averaged four per square foot in the

meadow, five per square foot in the pasture of scant vegetation, and eight per square foot in the pasture of abundant vegetation. Prof. Osborn (27) considers timothy the main host plant of this species, but timothy was abundant only in the meadow, where this leafhopper was least common. Sugarcane and rice are given as its host plants in Formosa, and it has an extensive distribution in Europe and Asia, presumably not being confined to one or a few grasses for its food.

The first nymphs were noted on May 15th, the last on August 4th. The first adult, a male, was collected on July 6th, the last male on August 22nd; the first female on July 17th, the last female on October 7th.

TABLE 18. Seasonal Abundance and Life History of *Acucephalus striatus.*

Number Collected	Period	Small Nymphs	Medium Nymphs	Large Nymphs	ADULTS		Number per square foot
					Males	Females	
2	April-May	2	..	..	..	..	.25
25	late May	25	..	..	..	..	2.5
123	early June	58	65	..	..	..	11.18
123	late June	..	49	74	..	..	12.3
88	early July	..	..	84	3	1	8.
90	late July	..	..	41	24	25	9.
18	early August	..	..	1	3	14	1.6
13	late August	..	..	..	2	11	1.6
14	September	..	..	..	..	14	1.
3	early October	..	..	..	..	3	.37
499		Total Nymphs: 399			Total Adults: 100		

One hundred sixty-three individuals of *Acucephalus albifrons* L., the next most abundant leafhopper, were collected from the hundred square feet. Only eight of this species were found in the pasture of scant vegetation, and only fifty-four in the meadow, the one hundred one remaining specimens being collected in the pasture of abundant vegetation, averaging 561 per hundred square feet, very considerably more than any other leafhopper in any other environment, but not as many as *Acucephalus striatus* in the same pasture. Prof. Osborn gives timothy as the hostplant, and calls this the Timothy Crown Leafhopper, but timothy was not especially abundant in this pasture, and doubtless the nymphs fed on bluegrass and redtop, which were four times and twice as abundant.

The first nymphs were noted on June 7th, the last one was seen on July 18th. The first adult seen was a female, collected on July 8th; the last female was noted on October 12th. Males were found from July 9th to August 16th.

The most abundant leafhopper in the meadow during August was the little *Xestocephalus pulicarius* Van Duzee, which probably feeds largely on orchard grass. One hundred individuals of this species were collected, 87 being found in the meadow. Between August 4th, when the first small nymphs

were noted, and September 20th, when the last adult was seen in the meadow, these leafhoppers averaged 543 per hundred square feet of meadow. The very small chalky grey nymphs were seen from August 4th to 30th, and adults from August 8th to October 7th, but possibly the first and smallest nymphs escaped observation, or occurred in areas which happened not to be examined.

TABLE 19. Seasonal Abundance and Life History of *Acucephalus albifrons.*

Number collected	Period	Nymphs	Males	Females	Number per square foot
9	late June	9	..	..	.9
42	early July	31	8	3	3.8
73	late July	29	36	8	7.3
25	early August	11	5	9	2.5
7	late August	..	1	6	.8
6	September	..	..	6	.4
1	early October	..	..	1	.1
163		80	50	33	..

Three species of the genus *Deltocephalus* were collected during the summer: 26 specimens of *Deltocephalus affinis* Gillette & Ball, 39 of *D. configuratus* Uhler and 22 of *D. inimicus* Say. *Deltocephalus inimicus* and *D. affinis* were nearly twice as abundant in the pasture of abundant vegetation as in either of the other two environments, but *D. configuratus* was taken only in the meadow, being noticeably abundant in areas where orchard grass occurred. As will be noted in Table 20, in which are given the first and last dates when nymphs and adults of each generation were collected, all three species have two generations during the summer, although no nymphs of the first generation of *D. inimicus* happened to be collected.

TABLE 20. First and Last Dates when Nymphs and Adults of Three Species of *Deltocephalus* were collected at Barneveld, N. Y.

	D. affinis		*D. configuratus*		*D. inimicus*	
	Nymphs	Adults	Nymphs	Adults	Nymphs	Adults
First brood	May 15	June 11	May 26	June 7	.....	July 20
	.....	July 3	June 29	July 18	.....	August 13
Second brood	July 4	.....	July 26	September 7	August 16	August 30
	August 22	October 8	August 15	September 11	September 10	October 3

Thirteen adults of *Athysanus curtisii* Fitch were collected during the summer, and one nymph on June 20th in the meadow. The adults were found almost entirely in the environments of abundant vegetation, from June 13th to September 19th. One *Thamnotettix inornata* Van Duzee and one *T. clitellarius* Say were collected July 20th in the pasture of abundant vegetation. Two specimens of *Phlepsius irroratus* Say were collected in the meadow on June 20th and July 3d.

Eleven individuals of *Balclutha impictus* Van Duzee were found during the latter part of the summer: nymphs from July 25th to August 22nd, and adults from August 12th to October 8th. This species prefers orchard grass and bluegrass in environments of abundant vegetation.

TABLE 21. Summary of Leafhoppers.

Total Number Collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
101 *Agallia 4-punctata*	43	47	11	84	151	60
16 *Kolla bifida*	15	..	1	29	..	5
32 *Draeculacephala m. minor*	25	3	4	49	10	22
499 *Acucephalus striatus*	203	153	143	400–	500–	600–
163 *Acucephalus albifrons*	54	8	101	106	26	561
100 *Xestocephalus pulicarius*	87	11	2	170	35	11
26 *Deltocephalus affinis*	13	6	7	25	20	38
39 *D. configuratus*	39	..	..	76	..	..
22 *D. inimicus*	9	6	7	18	20	38
14 *Athysanus curtisii*	10	1	3	19	3	16
2 *Thamnotettix* spp.	..	..	2	..	..	11
2 *Phlepsius irroratus*	2	..	..	4	..	..
11 *Balclutha impictus*	8	1	2	16	3	11
1027 leafhoppers	508	236	283	996	768	1583

A total of 1,027 leafhoppers for the hundred square feet, or 447,371 per acre, shows that this factor in the population of grasslands is of considerable importance, despite the comparatively small size of the individuals. As practically all feed on grass, they cause a direct loss to the farmer in reducing the amount of pasturage available for his cows, and in the hay he mows.

Aphïdae

One hundred twenty-four aphids of various species were found in the hundred square feet, being most abundant in the environments of abundant vegetation, especially in the meadow, where they average 165 per hundred square feet. In Illinois in a similar environment, they were nearly twice as abundant in the fall, winter and spring, averaging 278 for the same area. Sixty-two aerial aphids were found, of which 21 were *Macrosiphum pisi* Kalt., taken on red clover in the meadow from May 26th to September 17th, the last one collected being winged. On the other aerial aphids, 17 black ones on everlasting, collected September 8th in the pasture of abundant vegetation, were identified by Dr. A. C. Baker as *Macrosiphum ambrosiae* Thomas. The remainder of the aerial aphids were scattered individuals, of which the host plant was not noted with certainty.

The other half of the aphids were subterranean in habit. Two large purple ones collected May 16th and 12 light green ones collected July 16th were on the roots of red clover; 39 woolly white ones were on dandelion

roots June 20th, all collections being made in the meadow. These aphids were attended by 125 ants of the species *Lasius umbratus mixtus aphidicola* Walsh. Only 9 subterranean aphids were found unattended by ants; 7 large grey ones on the crown of a strawberry plant in the meadow, observed September 30th when it was so cold that insects moved with difficulty and no ants were out foraging for food, the other 2, of apparently the same species, but in the pasture of scant vegetation, where this kind of ant did not occur.

Coccidae

Eighty-eight mealybugs were found in the hundred square feet, being three times as abundant in the pasture of scant vegetation as in the other environments. In Illinois, the number of large mealybugs was 89 per hundred square feet, but of the eggs and young there were over a thousand for the same area. The difference was partly due to the time of year, but largely to the other species found.

Twenty-five of the 28 mealybugs found in the meadow at Barneveld were *Pseudococcus trifolii* Forbes, on the roots of red clover. Three others of this species were found on the roots of white clover August 3d in the pasture of scant vegetation. Fourteen mealybugs, found on grass in the pastures and in greatest abundance during September, were identified by Dr. Harold Morrison as *Trionymus americana* Cockerell. The other mealybugs were not identified. Seventeen pink ones were found in the roots of mint on September 6th in the pasture of scant vegetation, attended by ants, *Lasius americanus* Emery. In the same pasture, over 20 mealybugs were found in the soil from 2 to 6 inches down, and apparently not on roots.

TABLE 22. Summary of the Aphids and Mealybugs.

Total Number Collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
124 aphids	95	5	24	165	16	131
88 mealybugs	29	50	9	57	162	49

SUMMARY OF THE HEMIPTERA-HOMOPTERA

In the hundred square feet of grasslands, 66 predaceous bugs and 55 herbivorous bugs occurred, 19 planthoppers, 61 froghoppers, 29 treehoppers, 88 mealybugs, 124 aphids and 1,027 leafhoppers. Thus, in point of numbers, the leafhoppers constitute over two-thirds of the sucking insects present, and one species alone, *Acucephalus striatus*, of which 499 were found, over one-third of the total of 1,469. In size, most of the other sucking insects are no larger than these leafhoppers, and those stinkbugs (Penatomidae) which are considerably larger, in numbers are relatively insignificant.

LEPIDOPTERA

The total number of butterflies collected in the hundred square feet was only eleven, but these were not the only ones seen and habitually present in the pastures and meadow. Two adults and six larvae of the Hesperiid butterfly, *Polites peckius* Kirby, were found. The larvae are brown with a black head and a yellow and black ringed neck, and apparently feed on grass. Two adults of *Brenthis bellona* F. were collected May 31st in the meadow, but adults of *B. myrina* Cramer were also present and probably equally abundant. One chrysalis of *Argynnis cybele* F. was found May 31st in the meadow, and an empty chrysalis of *Pyrameis huntera* F. on everlasting Sept. 8th in the pasture of abundant vegetation. The other butterflies noted but not coming within the limits of the areas examined were: *Chrysophanus hypophlaeas* Boisduval, first noted June 12th; *Basilarchia arthemis* Drury, June 14th; *Satyrus alope* F., June 30th. *Colias philodice* Godart, the larva of which feeds on clover, was abundant in the part of the meadow near the gardens during the latter part of the summer, as was also *Pieris rapae* L.

Arctiidae

(All moths and some of their immature stages were determined by Dr. W. T. M. Forbes, of Cornell University.)

Six individuals of *Eubaphe immaculata* Reakirt were found: the first larva on July 14th in the meadow, a small brown pupa nine days later, and four other larvae in September and October, indicating the appearance of the adults in August. The black, hairy caterpillars are general feeders, but usually eat grass.

Noctuidae

Sixty-six Noctuids were found in the hundred square feet: 44 individuals of *Feltia venerabilis* Walker, 20 of an undetermined, glistening, light and dark golden brown striped larva tentatively determined as *Nephelodes minians* Guenee, 1 larva of *Mamestra* sp., and 1 adult of *Hadena devestatrix* Brace.

The larvae of *Feltia venerabilis* feed almost exclusively on the leaves of white clover, and its abundance in the various environments closely parallels the abundance of the host plant. The larvae remain hidden by day, feeding only at night, and it is only when the sod is dug up and picked to pieces that all the cutworms present, hiding between the clover stems and roots, are found. The first larva, collected April 23d in the meadow, was small; the next one found, on April 30th, was about half grown, and throughout May, partly to nearly fully-grown larvae were noted. On June 1st, in an area of the pasture of scant vegetation consisting almost entirely of moss, *Polytrichum* sp., two of these fully-grown larvae and two of *Nephelodes* were found, apparently already aestivating, and although larvae were found feed-

ing after that date, most of them were fully-grown and aestivating. From the first pupa found, on June 25th, an adult emerged July 14th, but other pupae were noted as late as August 21st and September 4th, and even large larvae up to this date. Adults were collected September 4th, 6th and 18th. From this rather fragmentary data, it would appear that there is but one generation a year, the period of aestivation may be only a few days or for as much as two months, with a corresponding variation of about two months in the time of pupation and the emergence of adults. Or it might indicate that the excessive losses suffered from the parasite, *Ophion bilineatus* Say, and from robins, so reduced the numbers of the cutworms during midsummer that none of the small larvae that should have appeared in July and August was observed.

Feltia venerabilis averaged 67 per hundred square feet in the pasture of scant vegetation, or 37,897 per acre. Yet not only was the white clover on which it fed apparently uninjured, but it furnished food for a number of other destructive insects, *Sitona hispidula*, *Sitona flavescens* and *Hypera punctata*, besides being one-sixth of all the vegetation in this pasture which the cows ate. (White clover was 11.2 percent of all vegetation, of which the species acceptable to the cows amounted to not more than 72 percent of the total vegetation present.) Despite all these handicaps, it was the most abundant plant in this pasture, truly a striking indication of the wonderful recuperative and growing powers of white clover in a suitable environment.

In an area especially selected as being as nearly as possible all white clover, examined on May 30th, ten larvae of *Feltia venerabilis* and one other cutworm were found, which would indicate that a pasture consisting entirely of white clover would contain 479,160 cutworms per acre. It is interesting to speculate whether that many cutworms would be present but very much the same result is obtained in another way. In ten square feet of unselected areas of this pasture examined between April 30th and June 14th (the first and last dates on which larvae were found) twelve cutworms were found. Of these areas the white clover constituted only 11.2 percent of the vegetation, but if it had been 100 percent of the vegetation, this would give 10.71 larvae per square foot, which is surprisingly close to the ten larvae of *Felitia venerabilis* actually collected in the selected area. It seems hardly possible for what appears to be such an enormous number of cutworms to be present without their presence being suspected, for in the area where the eleven were collected, the clover appeared to be without a break or any indication of the feeding of the cutworms. A drought might make the results of their presence obvious, but rainfall in May, 1919 averaged .15 inches per day, and their injuries could not be detected.

Eighteen of the glistening cutworms which were yellow in the earlier instars and later striped light yellow and purplish golden brown, tentatively determined as *Nephelodes minians* Guenee, were found in the hundred square

feet, and two pupae of this species, making an average of one to five square feet. The larvae feed on grass, and were of almost equal abundance in all environments. The first small larvae were noted early in May, and by the first of June fully-grown larvae had begun to aestivate, the first pupa being collected in early July. A larva collected July 15th pupated on August 12th, the adult emerging previous to September 10th, on which date it was found dead in the rearing cage, too battered for identification. No adults were collected in the field.

Only five unparasitized pupae of all Noctuids were found during the summer, while the collection of two parasitized pupae and five cocoons of *Ophion bilineatus* Say with only traces of the host larva or pupa remaining, indicate 60 percent parasitism by this one wasp. One of the 36 larvae of *Feltia venerabilis* found during the summer had two Tachinid fly eggs on its third thoracic segment, but the larva died a few days after its collection, and no other stage of this parasite was observed.

Geometridae

Three larvae of the large, grey, grass-feeding lopper, *Drasteria* sp., were found in the meadow, and an adult of *Pernoptilota fluviata* Hübner on August 11th.

Crambidae

One egg-cluster, 25 larvae and 2 adult Crambid moths were found in the hundred square feet. The two adults, collected June 18th in the pasture of scant vegetation, were *Crambus agitatellus* Clemens, but it is unlikely that all of the larvae were of this species, as five other Crambid adults were common at light at this date: *Crambus alboclavellus* Zeller, *C. hortuellus* Hübner, *C. laqueatellus* Clemens, *C. girardellus* Clemens and *C. mutabilis* Clemens, all determined by Dr. Forbes. Medium-sized to large larvae were found in the spring as late as June 1st, and adults were abundant in mid-June and later. "The eggs (of *Crambus* spp.) are very small and dropped indiscriminately by the female moths as they fly about over the grass at dusk and during the early hours of the night. Being dry, the eggs fall down among the grass stems and are therefore difficult to find." (1) A cluster of creamy, flattened eggs, similar in appearance to those of *Diatraea saccharalis* F., and obviously not any of the *Crambus* spp. of which adults were collected, was found on a daisy leaf June 24th in the pasture of scant vegetation. No larvae were noted during the middle of the summer until August 20th, but all sizes were found from then until the end of the investigation. On October 12th, two very small larvae were found, indicating that some at least of the species pass the winter as partly-grown larvae. The larvae live on the ground, making extended, tunnel-like shelters of debris, and usually feeding on grass. They were most abundant during October, when they averaged

slightly over one per square foot, and they were twice as numerous in the pasture of abundant vegetation as in the other environments.

An adult of *Sparganothis sulfureana* Clemens was collected August 3d in the pasture of scant vegetation, and in the same pasture on June 24th, an adult of *Platyptilia marginidactyla* Fitch, the larva of which bores in yarrow. A leaf-roller larva of cherry, four leaf-tier larvae on strawberry, buttercup, violet and clover leaves, and a leaf-roller larva on strawberry were the other larvae of which the host plant was noted, but which were not reared to adult. Forty-three other individuals of some stage of Lepidoptera, mostly very small larvae, were collected, but not identified or reared to adult.

TABLE 23. Summary of Lepidoptera.

Total Number Collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
1 *Argynnis cybele*	1	..	..	2	..	..
2 *Brenthis bellona*	2	..	..	4	..	..
8 *Polites peckius*	3	1	4	6	3	22
6 *Eubaphe immaculata*	4	2	..	8	6	..
20 ? *Nephelodes* ?	9	7	4	18	23	22
44 *Feltia venerabilis*	10	27	7	19	87	38
2 other cutworms	1	..	1	2	..	5
4 Geometrids	2	2	..	4	6	..
22 *Crambus* spp.	11	8	9	21	26	50
51 all others	27	12	12	53	38	66
166 Lepidoptera	70	59	37	137	189	203

DIPTERA

(All Diptera were determined by Prof. O. A. Johannsen of Cornell University.)

THE PREDACEOUS FLIES

One large mosquito, *Psorophora ciliata* F., the larva of which is predaceous on other mosquito larvae, was collected May 29th in the meadow. One Tabanid fly, *Chrysops niger* Macquart, was collected June 7th. These blood-sucking flies are predaceous on man and large domestic animals, and in this case the fly was attracted to the area under investigation by the presence of the investigator. The flies were more or less abundant all through the summer, and were especially troublesome on May 31st and June 12th. One Muscid fly, *Pollenia rudis* F., the larva of which is parasitic on earthworms, was collected Sept., 17th in the meadow.

Twenty-two Threviid larvae (*Psilocephala*), first determined by Mr. R. H. Van Zwaluwenburg, were found in the hundred square feet, being five times as abundant in the pastures as in the meadow. They are general predators on subterranean insects. One larva was found in dung, thirteen at a depth of two inches in the soil, and the remainder from three to five

feet, and two pupae of this species, making an average of one to five square feet. The larvae feed on grass, and were of almost equal abundance in all environments. The first small larvae were noted early in May, and by the first of June fully-grown larvae had begun to aestivate, the first pupa being collected in early July. A larva collected July 15th pupated on August 12th, the adult emerging previous to September 10th, on which date it was found dead in the rearing cage, too battered for identification. No adults were collected in the field.

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slightly over one per square foot, and they were twice as numerous in the pasture of abundant vegetation as in the other environments.

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2 *Brenthis bellona*	2	..	..	4	..	..
8 *Polites peckius*	3	1	4	6	3	22
6 *Eubaphe immaculata*	4	2	..	8	6	..
20 ? *Nephelodes* ?	9	7	4	18	23	22
44 *Feltia venerabilis*	10	27	7	19	87	38
2 other cutworms	1	..	1	2	..	5
4 Geometrids	2	2	..	4	6	..
22 *Crambus* spp.	11	8	9	21	26	50
51 all others	27	12	12	53	38	66
166 Lepidoptera	70	59	37	137	189	203

DIPTERA

(All Diptera were determined by Prof. O. A. Johannsen of Cornell University.)

THE PREDACEOUS FLIES

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Twenty-two Threviid larvae (*Psilocephala*), first determined by Mr. R. H. Van Zwaluwenburg, were found in the hundred square feet, being five times as abundant in the pastures as in the meadow. They are general predators on subterranean insects. One larva was found in dung, thirteen at a depth of two inches in the soil, and the remainder from three to five

inches down. They were collected from May 13th to September 6th, being most abundant in August. No puparia were found, nor were adults collected or reared.

One large Leptid larva, *Coenomyia ferruginea* Scopoli, was found two inches below the surface of the ground in the meadow on September 17th. Other Leptid or Asilid maggots were found from three to six inches down in the soil of the pastures, May 8th, July 2nd and 25th.

Nine Syrphid flies, the larvae of which are predaceous on aphids, and one larva, were found during the summer. Five adults of *Mesogramma marginata* Say were collected from July 18th to August 15th, the first one collected having a red mite clinging to it. Two adults of *Mesogramma politum* Say were collected September 8th and 20th, and one of *Melanostoma mellinum* L. on August 4th.

THE HERBIVOROUS AND SCAVENGER FLIES

Fifteen maggots of the crane fly, *Pachyrhina ferruginea* F., were found, two on June 6th and 18th, and none thereafter until September 12th, after which 13 were found in the 14 square feet examined. The maggots showed a very decided preference for the pastures, where they were six times as abundant as in the meadow. Whether the dung is responsible for this preference was not determined, as of the two areas containing old cow dung, examined September 18th and October 7th, one contained four maggots, the other none. The maggots live at or just below the surface of the ground, although one was found two inches down.

The maggots found in June pupated soon after collection and adults emerged in early July. Other adults were noted in some abundance at light during July and August. Mr. Hyslop (16) states that adults of this crane fly "are flying about in March and April", and that there is "a probable second brood . . . in August and September." "The larvae (of an undetermined species) which often occur in enormous numbers, as many as 200 having been found in an area covering a little over 1 square foot, feed upon the roots of various plants, seeming to prefer the Leguminosae, and . . . they not only suck the juices of the roots but devour the plant tissue itself. . . . They feed during the early fall and hibernate as half-grown larvae, resuming activities in the spring."

Similar maggots, *Bibio albipennis* Say, form the most important food of robins in early spring, February and March in Massachusetts and Illinois (14), but this species was not found in the grasslands at Barneveld, although it may have been abundant in the woods where the robins nested.

Forty-two individuals of the Clover Seed Midge, *Dasyneura leguminicola* Lintner, were found in the meadow where the red clover grew. Two larvae of the spring generation were noted on the ground in the first examination made, April 23d, but not one of the adults of this generation was noted. The

hay was cut in the meadow on June 23d, but several unmowed areas close to the fence containing red clover in blossom were examined after that date without finding the midge, until July 12th when 27 larvae were found in the clover heads. Single larvae were found on the ground from July 16th to August 11th, five on August 20th and three on the 21st. An adult of the second generation was collected August 13th.

Of 9 small flies collected in September and October, Prof. Johannsen determined three to be new species of *Neosciara,* and one to be *Sepsis violacea* Meigen. The larva of the latter feeds on dung. Three adults of *Tanytarsus dives* Johannsen were collected between July 26th and September 13th. Twenty-eight very elongate, transparent, black-headed larvae were found in the pasture of abundant vegetation in an area containing an abundance of moist moss and well shaded by high buttercup plants, but none was reared to adult. Twenty small pupariae were found in dead buttercup stems on July 8th in this pasture, but no adults emerged from them. One small green Dolichopodid fly was found August 12th in the pasture of abundant vegetation. The other Diptera found in the pastures consisted of larvae or pupae in cow dung, some of which were determined as *Scheophaga* sp.

TABLE 24. Summary of Diptera.

Total Number Collected	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
26 subterranean predaceous larvae	5	15	6	10	48	34
10 Syrphid flies	4	4	2	8	13	11
3 other predaceous	3	..	..	6	..	..
15 crane fly maggots	2	8	5	4	26	27
42 clover seed midge	39	3	..	76	10	..
126 herbivor or scavenger	27	26	73	47	89	403
222	80	56	86	156	189	473

COLEOPTERA

(Unless otherwise noted, the determinations of all beetles have been made by Dr. E. A. Schwarz, of the U. S. National Museum.)

Carabidae

Ninety-three Carabidae were found in the hundred square feet, of which 11 were larvae, and the remainder adults. In Illinois, where almost as many Carabids were found in the same area, nearly a third were larvae, possibly due to the observations being made during the fall, winter and spring. The Carabids were twice as abundant in the pasture of scant vegetation as in the meadow, and eight times as abundant in the pasture of abundant vegetation, although there was only one-third more insects there for them to feed upon. Robins, as later will be shown, are an important factor in limiting the

numbers of these beetles, and were probably responsible for the small number in the pasture of scant vegetation.

Dytiscidae

Two carnivorous diving beetles, *Hydroporus dichrous* Melsh., collected June 10th in the pasture of scant vegetation, and *Agabus* sp., a female in the meadow on June 11th, were several hundred yards from water.

TABLE 25. Summary of the Carabidae.

Total Number Collected	NAME	Date of First and Last Collection	Number found in:			Number in 100 sq. ft. of:		
			M	pSC	pAB	M	pSC	pAB
11	larvae		1	7	3	2	23	16
21	*Dyschirus globulosus* Say	May 23—Oct. 12	2	7	12	4	23	66
3	*Dyschirus longulus* Leconte	August 23	..	..	3	..	..	16
18	*Tachys vivax* Leconte	August 6-21	1	2	15	2	4	82
6	*Pterostichus sayi* Brulle	May 20—Oct. 1	2	..	4	4	..	22
3	*Amara* spp. (*obesa* ?)	June 3—July 18	3	..	..	6	..	..
2	*Badister notatus* Hald.	Aug. 13—Sept. 7	2	..	..	4	..	..
3	*Calathus opaculus* Leconte	June 17—Oct. 1	1	1	1	2	3	5
5	*Calathus gregarius* Say	August 4-29	1	1	3	2	3	16
1	*Platynus* sp.	September 30	1	..	..	2	..	..
1	*Platynus cupripennis* Say	October 12	..	..	1	..	..	5
3	*Lebia viridis* Say	May 13—July 16	3	..	..	6	..	..
1	*Cymindis pilosa* Say	August 16	..	..	1	..	..	5
1	*Chlaenius tomentosus* Say	July 23	..	1	..	..	3	..
4	*Harpalus pleuriticus* Kirby	June 23—Sept. 11	2	..	2	4	..	11
1	*Harpalus varicornis* Leconte	July 15	..	..	1	..	..	5
6	*Stenelophus conjunctus* Say	April 30—Oct. 1	1	2	4	..	6	22
3	*Stenelophus plebejus* Dej.	April 30—Sept. 6	..	3	..	..	10	..
93	Carabid beetles and larvae		19	24	50	38	75	282

Pselapidae

Three adults of *Decathron longulum* Leconte, very small brown beetles with clubbed antennae, were collected August 16th in the pasture of abundant vegetation. Of this family Blatchley (5) says: "They live for the most part beneath bark and stones, where they feed on minute *Acarina* and other minute animal forms."

Staphylinidae

One hundred fifteen Staphylinid beetles were collected in the hundred square feet, being nearly twice as abundant in the pasture of abundant vegetation, where they averaged 182 per hundred square feet, as in the other pasture or meadow. Apparently the combination of dung and abundant vegetation produces the most favorable environment, as these beetles feed on all sorts of decaying animal and vegetable substances. In the meadow on June 23d, towards the end of several weeks of drought during which very few Staphylinids had been noted, a swarm of a hundred or more medium to small Staphylinid beetles, of various species, swarmed over the hole and

pile of moist earth at the end of the examination, alighting on the freshly exposed earth and apparently attracted by it. The drought of early August only slightly reduced the midsummer abundance of these beetles, and it is uncertain whether they do, to any considerable extent, seek out the moister environments during dry weather.

Phalacridae

Four Phalacrid beetles were found in the meadow. Two were *Olibrus (Stilbus) nitidus* Melsh., and two *Olibrus apicalis* Melsh., collected between

TABLE 26. Abundance of Staphylinid Beetles compared with the Amount of Rainfall.

Period	Beetles per 100 sq. ft.	Average daily rainfall
April—May	200	.13 inches
late May	40	.15
early June	10	.02
late June	122	.13
early July	180	.21
late July	160	.10
early August	110	.02
late August	212	.14
September	71	.10
early October	52	.25

TABLE 27. Summary of Staphylinidae.

Total Number Collected	NAME	Date of First and Last Collection	Number found in:		
			Meadow	Scant Pasture	Abundant Pasture
28	*Atheta* spp.	April 23—Oct. 12	17	4	17
1	*Aleochara* sp.	May 15	..	..	1
1	*Leptacinius longicollis* Leconte	October 5	1	..	..
8	*Heterothops fumigatus* Leconte	Apr. 23—Aug. 21	4	3	1
3	*Philonthus thoracacius* Grav.	July 26—Aug. 29	1	1	1
2	*Philonthus brunneus* Grav.	May 15—June 18	..	1	1
2	*Philonthus lomatus* Erichson	June 4—Aug. 29	1	1	..
7	*Philonthus inquietus* Erichson	Apr. 30—July 23	..	3	4
5	*Philonthus* spp.	May 14—July 9	1	3	1
1	*Xantholinus obscurus* Erichson	April 23	1	..	..
6	*Xantholinus emmesus* Grav.	May 31—Sept. 13	4	1	1
1	*Xantholinus pusillus* Sachse	August 29	..	1	..
4	*Stenus* sp.	July 25—Oct 12	..	..	4
1	*Astenus (Sunius) discopunctatus* Say	August 12	..	..	1
2	*Cryptobium pallipes* Grav.	Apr. 30—May 16	1	1	..
2	*Cryptobium latebricola* Norden	July 23	..	2	..
1	*Cryptobium claricorne* Casey	August 13	1	..	..
2	*Lathrobium collare* Erichson	May 13—July 2	1	1	..
2	*Paederus littoralis* Grav.	July 9—Aug. 6	..	..	2
8	*Tachinus limbatus* Melsh.	Apr. 30—Aug. 30	4	1	3
3	*Tachinus fumipennis* Say	July 18—Sept. 7	..	3	..
25	*Tachyporus jocosus* Say	June 4—Sept. 20	13	8	4
115	Staphylinid beetles		53	31	31

the latter part of July and mid-September. According to Blatchley (5), the beetles "live principally on flowers, the larvae living in the heads of flowers, especially those of the Compositae."

Coccinellidae

Thirteen Coccinellid beetles were collected during the summer: 2 adults of *Hippodamia parenthesis* Say in the pasture of scant vegetation on July 13th and Aug. 14th, and 10 adults of *Hyperaspis undulata* Say, 9 of which were in the meadow, June 3d to September 17th, and 1 unidentified larva, probably of the latter species, found June 12th in the pasture of abundant vegetation. The greater abundance of aerial aphids in the meadow, especially of *Macrosiphum pisi* on red clover, possibly accounts for the greater number of lady-beetles found there, although in only one case were these beetles found in the same area with aphids.

Cryptophagidae

One specimen of *Tomarus pulchellus* Leconte was collected August 12th in the pasture of abundant vegetation near the creek.

Histeridae

Six Histerid beetles were collected: three of *Hister americanus* Payk., one April 23d in the meadow, and two May 23d in the pasture of scant vegetation, and three of *Hister abbreviatus* F. in the meadow on September 20th and 30th. For beetles that are supposed to live in animal excrement, it is rather surprising that twice as many should be found in the meadow as in the pastures. The first Histerid collected had two mites on it.

Nitidulidae and Carpophilidae

One Nitidulid, *Ips quadriguttatus* F., was collected June 4th in the meadow, and an unidentified Carpophilid on May 13th.

Elateridae

Eighty-three Elaterids were collected from the hundred square feet, being four and five times as abundant in the pastures as in the meadow. In the grassland areas examined in Illinois, vacant city lots, they averaged 55 per hundred square feet, as compared with 33 in the meadow at Barneveld, the most nearly comparable environment.

Mr. R. H. Van Zwaluwenburg determined an adult collected June 7th in the meadow as *Limonius griseus* P.B., 4 adults collected June 11th, August 23d and October 4th as *Monocrepidus auritius* Herbst, and 4 adults collected April 30th, May 21st, June 12th and October 3d as *Melanotus* probably *fissilis* (Say) Leconte. The remainder of the material consisted of larvae, some of which were determined by Mr. Van Zwaluwenburg as

Melanotus sp., and presumably most or all were of the above species. Four of the 74 wireworms were found on the surface of the ground, one-quarter of all were in old cow dung, one-half of all of them were two inches or less below the surface of the soil, 6 were three inches down, 3 were found four inches down and 2 were five inches down in the soil. Regarding the reason for the abundance of the Elaterid larvae in the dung, Mr. Van Zwaluwenburg writes: "The larvae of *Melanotus* are plant feeders and perhaps predatory on other small insects, at least they are cannibalistic. It is possible that they were under the dung looking for small dipterous larvae." There were comparatively few Dipterous larvae in the old cow dung, 23 being specifically recorded in or on it, possibly because the wireworms had destroyed most of them. It appears doubtful that the millipedes present in the dung could serve as wireworm food. Wireworms of all sizes were found from April 30th to October 7th, being most abundant in late May and early August, but this was probably only an accident of collection, for "the larvae spend two to five years in the soil" (17).

Byrrhidae

Two Byrrhid adults, *Cytlius sericeus* Forster, were found June 30th and July 15th in the pasture of abundant vegetation. Dr. Schwarz states that the beetle feeds on moss, of which a considerable amount was present in this pasture, although not in the areas where the beetles were collected.

Lampyridae

Twenty-five Lampyrids were found in the hundred square feet, being somewhat more abundant in the pasture of scant vegetation. In Illinois, thirty per hundred square feet were found. A large purple larva and a pink pupa which proved to be *Telephorus bilineatus* Say, were collected in the meadow on May 6th, and an adult was collected in the meadow on May 26th. Other larvae, not reared to adult, were found throughout the summer and autumn, the smallest one on May 30th, small ones from June 10th to July 25th, medium-sized larvae from August 3d throughout the month, with large larvae appearing in September and October. Two small larvae found October 7th were very probably of another species, possibly of *Silis bidentatus* Say, of which an adult was collected August 12th. The Lampyrids "are for the most part carnivorous in diet, especially in the larval stage, feeding mostly on small worms, larvae of other insects and snails."(5) Prof. Webster (37) records *Telephorus bilineatus* as "a powerful auxiliary in checking the ravages of the western locust."

Lamellicornidae

Two males and 3 females of *Onthophagus hecate* Panzer were found together in the pasture of scant vegetation on September 12th. There was

no dung in the area examined, and the beetles were half an inch below the surface of the ground. One of the females had four chestnut-colored mites clinging to her legs. *Copris minutus* Drury and *Copris anaglypticus* Say were also present in this pasture, but no specimens happened to occur in the areas examined.

Eight adults of *Aphodius fimetarius* L. were found between April and September in both meadow and pasture, and usually from three to six inches below the surface, although one was found on the surface of the ground. None occurred in old dung, and no fresh dung was examined. One adult of *Aphodius stercorosus* Melsh. was collected April 30th in the pasture of scant vegetation.

One adult of *Macrodactylus subspinosus* F., Fuller's rose beetle, was found in the meadow on June 17th, eating the disc flowers of a daisy head.

Twenty-five individuals of various stages of *Lachnosterna* were found in the hundred square feet. This is a comparatively small number, especially considering the proximity to woods of all fields examined, so small indeed that their injuries to the roots of plants in the grasslands are inappreciable to ordinary observation. To eat away the roots of sod so that it can be peeled off in rolls, these grubs should average five per square foot, or twenty times as abundant as at Barneveld, yet even scarce as they were here, they proved to be an important factor, largely because of their size. Mr. J. J. Davis determined one adult taken June 4th in the meadow as *Lachnosterna dubia* Smith, and another adult collected in the pasture of scant vegetation on June 18th as *L. fusca* Froelich. In a collection of 44 adults at light, Mr. Davis determined 6 males and 1 female as *L. dubia,* and 30 males and 7 females as *L. fusca,* giving some indication of the comparative abundance of the two species. In the list of trees on the leaves of which the adults of these two species feed, which Mr. Davis kindly prepared, are few of the trees of the region around Barneveld, but H. G. Crawford states that although he has collected both species most often on willow in Ontario, Canada, they also feed on grass and plantain.

Except for the two adults and one egg, two inches down, found August 3d, the other 22 records are of grubs, which were found at depths of from one to six inches. Three of the grubs were in first instar, May 23d to July 23d; 17 in the second, May 5th to October 1st, and two were in the third instar, May 28th and June 11th, but these data have little significance, for the life-cycle in this latitude requires three years.

Of the parasites of *Lachnosterna,* one adult of *Pyrgota undata* Wied., a Dipterous parasite of the adult, was taken at light early in June, but none was found in the areas examined. One female of *Tiphia transversa* Say, determined by Mr. A. B. Gahan, was found Sept. 8th in the pasture of scant vegetation, besides four cocoons, at other dates, from which the adults had emerged.

Chrysomelidae

Twenty-four little black-headed beetle larvae with their bodies enclosed in curious little oblong black or grey baskets, which they pull about with them on the surface of the ground, were found during the summer; only two in the meadow, but 22 in the pastures, and averaging one to two square feet there. The basket covering the larva is a development of the excrementitous covering enveloping the egg when deposited by the female (24). "When the larva hatches, it remains within this case, and subsequently enlarges it by additions from its own body." The adults developing from these basket-inhabiting larvae belong to various genera of the sub-family Captosomes. The adults collected were: *Graphops* sp., collected June 24th, *Graphops pubescens* Melsh., August 21st, *Graphops marcassitus* Crotch., October 1, *Pachybrachys hepaticus* Melsh., June 24th, and *Cryptocephalus* near *venustus* F., July 15th, making a total of 27 adults and larvae of this group of Chrysomelids in the 49 square feet of pasture.

Two adults of *Prasocuris varipes* Leconte were collected June 12th and 30th in the pasture of abundant vegetation, in buttercup flowers, covered with pollen, and apparently feeding upon it. The larvae live in aquatic plants.

One hundred seventy-seven individuals of *Phaedon aeruginosus* Suffrian, as determined by Mr. H. S. Barber, were collected in the hundred square feet. This is a broadly oval, convex, shining, bottle green (black) beetle, 3.5 mm. long and 2.5 mm. wide, the larvae of which feed on *Veronica officinalis* L. and *Veronica scutellata* L. It was but little more numerous in the pasture of scant vegetation than in the meadow, although *Veronica* forms almost as large a part of the total vegetation here as in the other pasture, where it averaged 717 per hundred square feet. An insignificant part of the meadow vegetation is *Veronica,* and apparently it thrives better where there is an abundance of other vegetation. The maximum number of beetles found in any one square foot was 53, on August 16th in the pasture of abundant vegetation, many of these being under the remains of large dead insects, grasshoppers and millipedes. This one collection comprises nearly half of all of these beetles collected in this pasture. The larvae, shaped somewhat like those of the Colorado potato beetle, but in color dark greenish-brown, spotted with dark brown, and usually more or less covered with dirt, were found from April 30th to May 23d. The first adult was collected June 17th, from which date adults were abundant till mid-August, and a few individuals were noted up to the last date on which observations were made, October 12th.

Dr. E. Porter Felt states that specimens similar to those from Barneveld have previously been collected in New York State by Mr. D. B. Young, on horseradish, at Newport in June 1898, and at Ilion in 1901, both villages in the adjoining (Herkimer) county. There are specimens in the National Museum which appear to be the same, from Cambridge, Mass., Buffalo, N. Y.,

and Circleville, Ohio, but they vary somewhat and may not all be the same, according to Mr. Barber. He further states that "they differ from three specimens labeled *aeruginosus* by Linell, and only a few, even of (the Barneveld) series, seem to agree with Suffrian's description." Dr. Chittenden records *Phaedon aeruginosus* as a pest of water-cress at Brandywine Summit, Pa., and at Springfield, Mass. (8), and in a later part of the same bulletin (9) from Halltown, W. Va. He figures and describes the larva, pupa and adult, but most of his notes are about a similar European species, *Phaedon armoraciae* L., the larvae of which feed on horseradish in England (25), and on *Veronica beccabunga* L. in Germany (10). It was as *Phaedon armoraciae* that the Barneveld specimens were at first determined, but from which they differ, according to Mr. G. E. Bryant of the British Museum, "in having the intervals on the elytra almost smooth and not nearly so strongly punctured." The similarity in the larval habits of the supposed two species, and the variation in the adults, suggests the possibility that all the records may be of but a single species.

Only ten flea-beetles (Halticini) were found in the hundred square feet, which is, according to Dr. Schwarz, entirely too low, and as in Illinois they averaged 154 for the same area, his comment seems pertinent. Seven adults of *Haltica rufa* Illiger were collected on the flowers of bluets May 8th in the pasture of scant vegetation. One yellowish-brown beetle, *Longitarsus* sp., was taken on August 16th, and two of the small black beetles, *Chaetocnema parcepunctata* Crotch, in the meadow on August 30th and September 11th.

Anthicidae

Six adults of *Notoxus anchora* Hentz, the beetle with "the thoracic horn which extends in sort of a hood over the head," were collected in the meadow, June 23d and July 3d. It is possible that two hairy larvae collected in the latter part of May were the immature stages of this beetle.

Eight larvae and one pupa, which were not identified, complete the total of the Coleoptera, exclusive of the Rhynchophora, found. Three of the larvae and the pupa died before transforming to adult, and five very small dark brown larvae found October 8th in the meadow, Dr. Schwarz could not identify.

Of the 623 beetles found, 136 are predaceous and therefore largely beneficial, 136 are scavengers, and, if anything, beneficial to man, 83 Elaterids are omnivorous, 196 are phytophagous feeding on weeds and are beneficial, 26 are phytophagous feeding on grass and grass roots and are harmful, 36 are phytophagous with food plant unknown, and 10 are unidentified, or habits unknown. That is: one twenty-fourth of the beetles in the grassland are definitely known to be undesirable and and harmful to the grass, the others being beneficial or neutral, or in the case of the wireworms, their status uncertain and dependent on circumstances. However, the May beetles and

white grubs, which numerically are such a small fraction of the beetles present, by weight constitute a larger part of the beetle population than all the others combined. No other beetle even approaches in size the *Lachnosterna* adult, and some adult beetles are even smaller than *Lachnosterna* eggs.

TABLE 28. Summary of the Coleoptera, exclusive of the Rhynchophora.

Total Number Collected	NAME	Feeding Habits	Number found in:			Number in 100 sq. ft. of:		
			M	pSC	pAB	M	pSC	pAB
93	Carabidae	usually predaceous	19	24	50	37	77	277
2	Dytiscidae	predaceous	1	1	..	2	3	..
3	Pselaphidae	predaceous	..	..	3	..	..	16
115	Staphylinidae	scavenger	53	31	31	104	100	172
4	Phalacridae	on daisy flowers	4	..	..	8	..	..
13	Coccinellidae	usually predaceous	9	2	2	18	6	11
1	Cryptophagidae		..	..	1	..	..	5
6	Histeridae	scavenger	4	2	..	8	6	..
1	Nitidulidae	phytophagous	1	..	..	2	..	..
1	Carpophilidae	scavenger	1	..	..	2	..	..
83	Elateridae	omnivorous	17	39	27	33	126	150
2	Byrrhidae	on moss	..	..	2	..	..	11
25	Lampyridae	predaceous	10	11	4	19	35	22
5	*Onthophagus*	scavenger	..	5	..	..	16	..
9	*Aphodius*	scavenger	5	4	..	10	13	..
1	*Macrodactylus*	on daisy flowers	1	..	..	2	..	..
25	*Lachnosterna*	phytophagous	9	13	3	18	42	16
28	Captosomes		2	16	10	4	51	55
2	*Prasocuris*	on buttercup flower	..	..	2	..	..	11
177	*Phaedon*	*Veronica*	29	19	129	57	61	717
10	Halticini	phytophagous	2	7	1	4	23	5
8	*Notoxus*	phytophagous	7	1	..	14	3	..
9	unidentified		7	1	1	14	3	5
623	beetles or their larvae		181	176	266	356	565	1473

Rhynchophora

Of the 515 Rhynchophora found in the hundred square feet, all were of the Curculionidae, and nearly three-fourths were Otiorhynchids or of the Sitonini group, the "Naupactides" of Lacordaire, which are similar in general appearance and in having subterranean larvae and pupae. Nearly half of the beetles of this group were found as larvae or pupae. Of these, only two were successfully reared to adult, for the mortality due to disturbance, slight injuries and mold was high. These two proved to be *Phyxelis rigidus* Say, but as adults of this species comprised but a small part of this group, the other larvae and pupae have been arbitrarily assigned to species in proportion to the abundance in which the adults were collected.

The few grubs found in late April were probably the hibernating larvae of *Phyxelis rigidus* Say, *Sciaphilus muricatus* F., or *Sitona flavescens* Marsham. Larvae were most abundant in the latter part of May, as the eggs laid by the two most abundant Curculionids, *Chaetechus setiger* Horn and *Sitona hispidula* F., which had hibernated as adults, began to hatch. The decrease

in the number of larvae in early June coincides with the appearance of pupae, and most of the larvae have pupated by mid-July. The increase in numbers of larvae beginning in late August represents the newly-hatched grubs of the species which hibernate in this stage.

Twenty-seven individuals of *Phyxelis rigidus* Say (13 adults, 2 larvae reared to adults and 10 larvae and 2 pupae arbitrarily assigned to this species) were collected in the hundred square feet. Adults were five and six times as abundant in the pasture of abundant vegetation as in the other environments, and were collected from June 23d to October 12th, the late record of the first adult indicating hibernation of the species as partly-grown larvae. The two larvae collected in the meadow on July 5th transformed to adults August 3d, and although adults were collected on the same date as the larvae, it is doubtful if there is more than one generation a year. Two dead adults found July 20th and September 19th, with round holes in their elytra, had probably been parasitized.

TABLE 29. Seasonal Abundance of Otiorhynchinae and *Sitona* spp.

Period	Larvae	Pupae	Adults
April-May	2	..	12
late May	43	..	7
early June	33	3	9
late June	22	6	12
early July	19	10	24
late July	6	3	19
early August	5	2	35
late August	8	..	28
September	11	..	36
early October	13	..	9
	160	24	189

Two adults (and 2 arbitrarily assigned larvae) of *Otiorhynchus ovatus* L. were collected in the meadow June 29th and August 11th. There were wild strawberry plants in the area examined in June, and as they constituted six percent of the vegetation in the meadow, it is rather surprising that this common pest of cultivated strawberries was not more abundant.

Sixty-seven adults (and 55 larvae and 9 pupae) of *Chaetechus setiger* Horn, were collected, being of about equal abundance in all environments. Adults were collected from April 23d to October 5th, with varying abundance through the summer, indicating hibernation of adults and possibly two generations a year, as no adults were found in the latter part of July. The greatest number of individuals found in one square foot was four, so there is no indication of what the host plant of the adults might be, and the beetle is so small that its feeding injuries were not noticed. The beetle is easily recognized by its small size, length 2 to 2.5 mm., and uniform brown color. Despite its great abundance at Barneveld, apparently little is known about it, and it is recorded by Blatchley and Leng as rare and confined to eastern Massachu-

setts and Nova Scotia. Only a few specimens were in the collection of the National Museum, and Dr. Felt writes that there are no records of it in the New York State Museum.

Five adults (and 5 larvae) of *Trachyphloeus davisi* Blatchley, or some closely allied species according to Dr. Schwarz, were found, 2 on April 23d and 2 on October 3d in the meadow, and 1 in the pasture of scant vegetation on July 23d. The specimens from which the beetle was described were collected on the sea beach at Ft. Wadsworth, N. Y., washed ashore from the ballast of some ship according to Mr. Barber, but the species is now firmly established in the United States to occur several hundred miles inland and two miles from a railroad. Adults were abundant at Remsen, N. Y., seven or eight miles north of Barneveld, in May 1922, in an old farmhouse, but the host was not observed. Undoubtedly the adults hibernate, and possibly there are two generations a year, adults of the first brood appearing in late July.

Eleven adults (and ten larvae and one pupa) of *Sciaphilus muricatus* F. were collected from June 29th to October 9th. As 7 of the adults were found in August, the species probably passes the winter in the larval stage and has but one generation a year. All except two of the adults were found in the meadow, usually in an area where several other Otiorhynchids were present.

Sixty-eight adults (and 57 larvae and 9 pupae) of *Sitona hispidula* F., and 23 adults (and 19 larvae and 3 pupae) of *Sitona flavescens* Marsham (determinations by the writer) were collected in the hundred square feet. These two beetles, closely resembling each other and both serious pests of clover, show interesting differences of habitat preference. *Sitona hispidula* was nearly as abundant in the meadow as in the pastures, and probably feeds on both red and white clovers, but only one of *Sitona flavescens* was found in the meadow, and that was close beside the pasture fence. Obviously, in this locality at least, *Sitona flavescens* avoids red clover and feeds only on white clover. It was only one-third as abundant in the pasture of scant vegetation as in the other pasture, but there, in an environment to which it is apparently well adapted, it was practically as numerous as the more common species.

Fifty-three individuals (19 larvae, 3 pupae and 31 adults) of *Hypera punctata* F. were collected in the hundred square feet, but only five of these were in the meadow, the others being in the pastures giving an average there of one per square foot. No larvae were found in the meadow, showing an absolute avoidance of red clover and a preference for the white clover of the pastures, corresponding to the observations of Prof. Webster (38) in Ohio, but Prof. Folsom (13) states that "in central Illinois, red clover is most heavily infested, alfalfa coming second and white clover third." Sixteen larvae and 3 cocoons, of which one was empty, were found in the pasture of scant vegetation, and only 3 larvae and 1 cocoon in the pasture of abundant

vegetation. The scarcity of the immature stages except in the environment of short vegetation may be due to the inroads of the fugus, the effects of which would doubtless be more severe in destroying the larvae where the vegetation is tall and abundant and does not dry out so promptly. All stages averaged twice as abundant in the pasture of scant vegetation.

The first larva noted, on May 8th, was half grown. The last larva was seen on June 14th, and cocoons were collected on June 6th, 14th and 25th. The first adult was collected on May 27th, the last on September 8th, and they were quite abundant in the latter part of July and moderately abundant throughout August.

Twenty beetles and 3 larvae of the genus *Phytonomus* were found in the hundred square feet, all except two in the meadow, so it is evident that red clover is the preferred host. The 3 larvae, one small and two large, were noted on May 26th. The first adult was collected June 29th, the last October 1st. All the beetles may be *Phytonomus nigrirostris* F., but by the key in Blatchley and Leng (6), 7 are *Phytonomus polygoni* F., 4 *P. meles* F., and 8 *P. nigrirostris*, all imported clover pests.

Of another imported clover pest, *Tychius picirostris* F., a slender grey beetle, 2.3 mm. to 2.5 mm. long, 19 adults were collected. All were in the meadow, indicating red clover as its only host. Beetles were collected from July 3d to September 7th, but over two-thirds of them were taken before the middle of July. The larvae were not observed.

Five adults of *Odontorhynchus salebrosus* Casey were collected, 3 in the meadow on June 29th and 2 in the pasture of scant vegetation of July 2nd.

Thirty-two individuals of *Ceuthorhynchus marginatus* Paykull were found, all in the meadow except one, and that one near the meadow fence. It should be noted that large dandelions, maturing large flowers, the host of the larvae, grew only on the meadow. Eight partly-grown maggots were found in the flower-head of a dandelion on June 3d, and one in another flower of the same plant, but two were uninfested and two others had ripened and scattered seeds. In the head containing the eight maggots, they had destroyed all the seeds. The first adult transforming from these maggots appeared on July 2nd, although in the field, adults were collected from May 26th to October 5th. The beetle is black, with a "conspicuous oblong sutural white spot immediately behind the scutellum." Mr. Hyslop (18) has written an interesting account of this beetle, the observations being made near Oneida Lake, at the opposite end of the county from Barneveld.

Ten adults of *Rhinoncus pyrrhopus* Boheman, determined by Dr. Schwarz, were collected, 5 in the pasture of scant vegetation and 5 in the meadow, from April 30th to August 21st. It "occurs mainly in different species of dock *(Rumex);* breeds also on smartweed" (6).

Of the 13 species of Curculionids found in the grasslands at Barneveld, the last three have larvae which feed on weeds, or at least the adults have been

collected on weeds or plants of no economic value, and thus these 47 individuals may be classed as beneficial phytophagous species. The 5 species feeding on clover, of which 74 individuals were collected, are all serious pests of decided economic importance. *Otiorhynchus ovatus* is a pest of cultivated strawberries, but is beneficial in grasslands. The larvae of the 4 remaining species feed impartially on the roots of whatever happens to be growing in the soil where they happen to be, yet in proportion as economic plants have their roots in the soil, these species are harmful plant feeders, and may be classed as such.

TABLE 30. Summary of the Curculionidae.

Total Number Collected and Name	Number found in:			Number per 100 sq. ft. in:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
13 *Phyxelis rigidus* Say	4	2	7	8	6	38
2 *Otiorhynchus ovatus* L.	2	..	..	4	..	..
67 *Chaetechus setiger* Horn	38	18	11	74	58	61
5 *Trachyphloeus davisi* Blachley	4	1	..	8	3	..
11 *Sciaphilus muricatus* F.	9	..	2	18	..	11
68 *Sitona hispidula* F.	30	23	15	58	74	83
23 *Sitona flavescens* Marsham	1	8	14	2	26	77
160 Larvae in soil	41	86	33	80	277	181
24 pupae in soil	14	6	4	27	20	22
53 *Hypera punctata* F.	5	36	12	10	116	66
23 *Phytonomus* spp.	21	1	1	41	3	5
19 *Tychius picirostris* F.	19	..	..	37	..	..
5 *Odontorhynchus salebrosus* Casey	2	3	..	4	10	..
32 *Ceuthorhynchus marginatus* Payk.	31	1	..	61	3	..
10 *Rhinoncus pyrrhopus* Boheman	5	5	..	10	16	..
515 Curculionidae	226	190	99	442	612	544

HYMENOPTERA

Tenthredinoidea

Nine sawfly larvae, identified by Mr. S. A. Rohwer of the U. S. National Museum, as *Dolerus* sp., were collected in the hundred square feet, occurring in the largest numbers in the environments of abundant vegetation. Those found during June were feeding on grass blades, but during August, September and October, they were two to four inches below the surface of the soil, apparently attempting to pupate. No adults were collected. Two cocoons, which Mr. C. F. W. Muesebeck thought to be of these sawflies, but from which no adults emerged, were found on the surface of the ground in the pasture on August 12th and 21st.

Ichneumonoidea

Of the parasitic Hymenoptera, nearly half of the individuals were *Ophion bilineatus* Say, as determined by Mr. C. F. W. Muesebeck. This is a common parasite of the larger lepidopterous larvae, and in these grasslands was

parasitic on the larvae of *Feltia venerabilis* and other cutworms. Seven cocoons, or parasitized Noctuid pupae, were found from June 24th to August 29th, from which this parasite emerged.

Of the other Ichneumonids, Mr. R. A. Cushman determined *Colpognathus helvus* Cresson collected in the meadow on April 23d, *Colpognathus fungor* Norton in the abundant pasture on August 6th, *Amblyteles detritus* Brulle on June 7th in the meadow and another *Amblyteles* sp. in the scant pasture October 7th. Mr. Muesebeck determined *Apanteles trachynotus* Viereck from the scant pasture on June 10th, *Apanteles ensiger* Say, a parasite of Crambid larvae, collected in the meadow on June 23d.

Chalcidoidea

Mr. Rohwer determined a small black Chalcid collected in the pasture of scant vegetation August 14th as *Eurytoma* sp., and two others from the meadow, August 13th and October 8th, were not identified.

Formicoidea

(All ants were identified by Prof. Wm. M. Wheeler, of Harvard University.)

Thirty-six workers of *Ponera coarctata* Latreille subsp. *pennsylvanica* Buckley were found in the hundred square feet, being nearly three times as abundant in the pastures as in the meadow. No immature stages were noted. Adults were collected from May 5th to September 20th. One worker of *Cremogaster lineolata* Say was collected May 29th in the meadow. Six workers of *Stenamma brevicorne* Mayr were found, 3 on July 18th in the meadow and 3 on September 6th in the pasture of scant vegetation. Nine workers of *Aphaenogaster fulva* Roger subsp. *aquia* Buckley were collected, 3 in the meadow May 21st, August 11th and 22nd, and 6 in the pasture of scant vegetation on June 14th.

Seventy-five individuals of *Myrmica brevinodis* Emery var. *canadensis* Wheeler were found between June 3d and September 6th. Only four of this species were collected in the meadow. A colony containing 29 adults and 12 pupae was found in the pasture of scant vegetation, six inches below the surface, on June 28th, making the species appear nearly twice as abundant here as in the other pasture.

Adults of *Myrmica scabrinodis* Nyl., subsp. *schencki* Emery, var. *emeryana* Forel were found from April 23d to October 4th, a total of 463 individuals for the hundred square feet. This species showed a decided preference for the environments of abundant vegetation, as workers were two and three times as abundant there, and no immature stages were found in the pasture of scant vegetation. A colony of 24 adults was found May 5th in the meadow, one inch below the surface of the ground; the first with immature stages in it on June 23d, two or three inches down, and others in August, one and a half to two or three inches below the surface. Fifteen winged adults were

noted in a colony August 6th, one inch down in the pasture of abundant vegetation.

The most abundant ant was *Brachymyrmex heeri* Forel, subsp. *depilis* Emery, of which 507 individuals were noted. All except 14 of these ants were found before June 28th, and during the period before this date they averaged 15 per square foot. The excepted 14 were collected August 16th to 23d in the pasture of abundant vegetation, where none at all of this species was noted during the spring. The immature stages were twice as abundant in the pasture of scant vegetation as in the meadow, but the foraging workers were twice as abundant in the meadow as in this pasture. Winged adults were collected April 23d, and immature stages from May 16th to June 28th. The colonies found in May were three to five inches below the surface, but the one broken into towards the end of June was only an inch down.

Lasius niger L., subsp. *alienus* Forster, var. *americanus* Emery was second in point of numbers found: 452. Of these, only 48 foraging workers were found in the environments of abundant vegetation. In the pasture of scant vegetation, 256 adults and 148 immature stages were collected, averaging 13 per square foot. Colonies were found from May 28th to October 4th, usually under stones.

Lasius umbratus Nyl., subsp. *mixtus* Nyl., var. *aphidicola* Walsh shows a very decided preference for the meadow, possibly largely because colonies of subterranean aphids occurred there. Of the 139 workers of this species collected, only two were in the pastures, and 123 were attending colonies of aphids. No immature stages were found. Adults were collected from May 16th to September 9th. The two workers found in the pasture were attending mealybugs, and were collected June 1st.

Seventeen of the large black *Formica fusca* L., var. *subsericea* Say were collected, being most abundant close to the woods in the pasture of abundant vegetation. Workers were noted from May 14th to September 8th, but no immature stages were found. One winged adult was collected August 21st in the pasture of scant vegetation, and in the same area were two workers which carried away an adult of *Hypera punctata* and a Capsid bug, which had not recovered from the anaesthetic as promptly as had the ants.

Seventy-seven workers of *Formica neogagates* Emery, a large dark ant, were found from May 5th to September 9th, being most abundant in the pasture of abundant vegetation, where they averaged 2 per square foot. No immature stages were noted.

The total number of ants found, 1,782, an average of nearly 18 per square foot, exceeds that of any other form of animal life. Especially in the pasture of scant vegetation, where, due to the preference for this environment by *Brachymyrmex depilis* and *Lasius americanus*, they averaged 2,664 per hundred square feet, they constitute in point of numbers nearly one-half of

all animals. In Illinois, the ants averaged 698 per hundred square feet, or only about half their number in the meadow at Barneveld, but this was possibly due to the time of year when that investigation was conducted: October to May.

Lasius aphidicola was the only one of the eleven species of ants that cared for and obtained nourishment from aphids. And it attended only the subterranean aphids, neither it nor any other species being observed to have any relations with the aerial aphids, or the mealybugs. The other ants were either largely or entirely scavengers, and their occurrence in such large numbers is possible only because of their small size. As the total of all aphids and mealybugs, minus the 60 subterranean aphids and mealybugs attended by *Lassius aphidicola,* amounts to only 150 individuals, it is hardly likely that the other 1,643 ants could be largely, if at all, dependent on them for food supplies, even though, under other environments, some of these species of ants are noted for fostering aphids. For the purposes of this investigation, all ants with the exception of *Lasius aphidicola,* will be considered as scavengers, and if anything, beneficial to the economic grasses and clovers.

Vespoidea

One Dryinid collected June 13th in the meadow Mr. Rohwer determined as *Anteon* sp. nov. Mr. A. B. Gahan determined as *Tiphia transversa* Say the single Scoliid wasp collected September 8th in the pasture of abundant vegetation. Other individuals were noted, not in the areas examined, during August. Four cocoons from which the adults had emerged were found in the areas examined, possibly an indication that the scarcity of white grubs in the grasslands at Barneveld at this time might be due to their effective control by this parasite.

Apoidea

(All bees were identified by Mr. J. C. Crawford, of the U. S. National Museum.)

A female of *Halticus pectoralis* Smith was collected on June 7th in the meadow. All the other Halticids were collected in the pasture of scant vegetation, where the ground was more exposed for the building of their tunnels. Two males of *Halticus provancheri* Dalla Torre and two of *Augochlora confusa* Robertson were collected August 14th, and another male of the latter species on mint flowers on September 6th. A female of *Halticus* sp. was collected August 29th. One honey bee, *Apis mellifera* L., was collected in the meadow on August 8th. Two small white hymenopterous maggots found May 23d in the pasture of scant vegetation could not be identified, nor a pupa in the meadow on September 30th.

TABLE 31. Summary of the Hymenoptera.

Total Number Collected and Name	Number found in:			Number in 100 sq. ft. of:		
	Meadow	Scant Pasture	Abundant Pasture	Meadow	Scant Pasture	Abundant Pasture
11 sawflies	4	2	5	8	6	27
13 Ichneumonid wasps	6	5	2	12	16	10
3 Eurytomid wasps	2	1	..	4	3	..
2 Sphecid wasps	1	..	1	2	..	5
8 bees	2	6	..	4	20	..
3 unidentified	1	2	..	2	6	..
1782 ants, as follows:						
36 *Ponera pennsylvanica* Buckley	9	17	10	18	55	55
1 *Cremogaster lineolata* Say	1	..	..	2	..	..
6 *Stenamma brevicorne* Mayr	3	3	..	6	10	..
9 *Aphaenogaster aquia* Buckley	3	6	..	6	20	..
75 *Myrmica canadensis* Wheeler	4	54	17	8	174	94
463 *Myrmica emryana* Forel	240	84	139	471	271	772
507 *Brachymyrmex depilis* Emery	271	226	10	531	729	55
452 *Lasius americanus* Emery	7	404	41	13	1303	227
139 *Lasius aphidicola* Walsh	137	2	..	268	6	..
17 *Formica fusca* L.	7	5	5	13	16	27
77 *Formica neogagates* Emery	15	25	37	29	80	205
1782 A N T S only	697	826	259	1364	2664	1435
40 other Hymenoptera	16	16	8	32	51	42

SUMMARY OF THE INVERTEBRATE POPULATION

A total of 6,843 invertebrates was collected from the hundred square of grasslands at Barneveld, New York, averaging 63.23 per square foot of meadow, 66.74 per square foot of pasture of scant vegetation and 86.74 per square foot of pasture of abundant vegetation.

SEASONAL VARIATION IN POPULATION

Seasonal variation in the population of the grasslands at Barneveld was considerable, but in the bulk was meaningless. Parasites, predators, disease and unfavorable weather and other environmental conditions tend to reduce the number of individuals of each species of insect or other invertebrate as those of each generation approach maturity. But unless the members of one group of the species having similar life-histories, such as: those hatching from eggs in the spring and becoming adult during the summer, constitute a large part of the total population, their decreases will be neutralized by the maximum of another group, or of other groups, with different types of life-histories. During June and July, an enormous number of leafhopper nymphs were present, especially in the pasture of abundant vegetation, but comparatively few transformed to adults and very few lived long after becoming adult. During cold weather, few ants go out on foraging expeditions, and unless a colony happens to occur in the area examined at this time, there

will appear to be less ants present. The comparative rarity during early spring and late fall of these two classes of insects which are so abundant during the summer is largely responsible for the seasonal variations in the grassland populations.

THE FACTORS IN THE ENVIRONMENTS AFFECTING THE ANIMAL POPULATIONS

The significant data on variation in abundance due to environment have been given under the heading of the individual, or group of species concerned. However, by grouping according to the environment the animals which were most abundant there, the characteristic factors of the environment influencing the composition of its animal population are brought out:

As might be expected, most of the animals are most abundant where there is the greatest abundance of their hosts, or food plants. In only the case of the Carabid beetles does abundance appear to depend upon scarcity of the animal predaceous upon them, although this factor also may explain the numbers of some others, at least in part. For those to which high vegetation is an important factor, this is often quite as much a response to protection from drying out as to abundance of food. Pasture versus meadow, because of the presence of cow dung, is the preference of animals living on or feeding

TABLE 32. Animals Most Abundant in the MEADOW at Barneveld, New York.

ANIMAL	Number in 100 sq. ft. of:			Factor Causing Abundance
	Meadow	Scant Pasture	Abundant Pasture	
molluscs	218	12	61	Orchard Grass
millipedes	777	355	678	high vegetation
sowbugs	215	10	55	Orchard Grass
all spiders	528	351	494	unknown
Argiope spp. (spiders)	12	6	0	unknown
Erigoninid spiders	363	129	237	unknown
same, minus *Erigone autumnalis*	353	110	182	unknown
Attid spiders	14	10	0	unknown
the following leafhoppers:				
Kolla bifida	51	16	22	high grass
Draeculacephala minor	49	10	22	high grass
Xestocephalus pulicarius	170	35	11	Orchard Grass
Deltocephalus configuratus	76	0	0	Orchard Grass
Balclutha impictus	16	3	11	high grass
the froghopper, *P. spumarius*	51	16	22	unknown
all aphids	165	16	121	specific hosts
Red Clover Aphis, *M. pisi*	41	0	0	Red Clover
Red Clover Mealybug, *Pseudococcus trifolii*	49	10	0	Red Clover
Red Clover Midge, *Dasyneura leguminicola*	76	10	0	Red Clover
Coccinellid beetles	18	6	11	Aphids
Notoxus anchora (beetle)	14	3	0	unknown
Phytonomus spp. (weevils)	41	3	5	Red Clover
Tychius picirostris (weevil)	37	10	0	Red Clover
Ceuthorhynchus marginatus	61	3	0	large Dandelions
Lasius aphidicola (ant)	268	6	0	subterranean Aphids

TABLE 32 *(cont'd)*

ANIMALS MOST ABUNDANT IN THE PASTURE OF SCANT VEGETATION

ANIMAL	Number in 100 sq. ft. of:			Factor Causing Abundance
	Meadow	Scant Pasture	Abundant Pasture	
Asagena americana (spider)	0	12	0	unknown
Gamasidae (mites)	49	116	39	unknown
Tomocerus flavescens (springtail)	49	100	39	unknown
Acalypha lillianis (flat bug)	0	16	0	Moss & Lichens
Agallia 4-punctata (leafhopper)	84	151	61	White Clover
Philaenus lineatus (froghopper)	16	38	22	unknown
Feltia venerabilis (cutworm)	19	87	38	White Clover
Psilocephala (Threviid) larvae	8	42	38	Pasture vs. Meadow
Telephorid (fire-fly) beetles	19	35	22	unknown
Onthophagus hecate (dung beetle)	0	16	0	Dung
Lachnosterna spp. (white grubs)	18	42	16	unknown
Haltica rufa (flea-beetle)	0	23	0	Bluets
Hypera punctata (clover weevil)	10	116	66	White Clover
Brachymyrmex depilis (ant)	531	729	55	short vegetation
Lasius americanus (ant)	13	1303	227	short vegetation
Myrmica canadensis (ant)	8	174	94	short vegetation
Halictus spp. (burrowing bees)	2	20	0	exposed soil

ANIMALS MOST ABUNDANT IN THE PASTURE OF ABUNDANT VEGETATION

ANIMAL	Number in 100 sq. ft. of:			Factor Causing Abundance
	Meadow	Scant Pasture	Abundant Pasture	
earthworms	92	110	166	unknown
Mermis spp. (hairworms)	35	26	44	Host Grasshoppers
Erigone autumnalis (spider)	10	19	55	unknown
Xysticus spp. (crab spiders)	21	35	66	Leafhoppers
Erythraeidae (mites)	101	29	232	Host Leafhoppers
grasshoppers	65	29	150	High Vegetation
crickets	70	74	377	High Vegetation
Nabis subcoleopteratus (bug)	4	10	27	Leafhoppers
Miris dolobratus (Capsid bug)	16	6	22	High Grass
the following leafhoppers:				
Acucephalus striatus	400–	500–	800–	Abundant Grass
Acucephalus albifrons	106	26	561	Abundant Grass
treehopper, *Entylia carinata*	0	0	44	Canada Thistle
Crambid webworms	21	26	50	High Grass
crane-fly larvae	4	26	27	Pasture vs. Meadow
Carabid beetles	37	77	277	Fewer Robins
Staphylinid beetles	104	106	177	unknown
Elaterid larvae (wireworms)	33	126	150	Pasture vs. Meadow
Phaedon aeruginosus	57	61	717	*Veronica* & ?
Sitona flavescens (weevil)	2	26	77	White Clover
Phyxelis rigidus (weevil)	8	6	38	unknown
Myrmica emeryana (ant)	471	271	772	Dung & High Grass (?)
Formica neogagates (ant)	29	80	205	Dung & High Grass (?)

in dung. The response of the cornfield ant, *Lasius americanus*, and of the burrowing bees to exposed soil and short vegetation is natural. Some of the apparent responses are undoubtedly accidents; the explanation of others would be simple if more were known of the food and habits of the animal.

The most obvious conclusion to be drawn from these data is that each animal occurs where its food is most abundant, and usually its adaptations are to the environment where this food is most common.

THE ECOLOGICAL FUTILITY OF THE SYSTEMATIC GROUPING

From Table 33, in which the total number of animals, arranged systematically, found in each environment, is given, it will be noted that the insects constitute three-fourths of all animals found. And of the insects, the ants, numbering 1,782, and the leafhoppers, numbering 1,027, are over half the total. But the systematic grouping, although possibly interesting in itself, serves no ecological purpose. Forms of quite divergent habits are often in the same taxonomic group, and even when systematically similar animals happen to have similar habits, undue prominence is given to the more numerous but smaller organisms. Even multiplying the numbers of similar animals by their weight does not give an altogether adequate idea of their relative importance. Each organism is of importance as it vitally affects the greatest number of other organisms: that is, as it takes the largest share in destroying its host or hosts, and in furnishing a supply of food for other organisms.

TABLE 33. The Animals found in the Grasslands at Barneveld, New York.

Phylum	Class	Number found in:			Total for the 100 sq. ft.
		Meadow	Scant Pasture	Abundant Pasture	
Vermes	Nematoda	26	12	8	46
Anellida	Chaetopoda	47	34	30	111
Mollusca	Gastropoda	110	4	11	125
Arthropoda	Crustacea	110	3	10	123
	Arachnida	349	155	140	644
	Myriapoda	394	109	120	623
	Insecta	2189	1752	1230	5171
		3225	2069	1549	6843

THE ECOLOGICAL IMPORTANCE OF THE SMALLER ANIMALS

Of the smaller animals, the millipedes, despite their relatively great size and abundance, have little direct effect on other living organisms, and themselves form an insignificant part of the food of any other animal. Great numbers of their bleached exoskeletons were noted in making the examinations, and the reports of economic ornithologists show that few birds eat them, and even then they form not more than two or three percent of the total food eaten. Slugs, snails and sowbugs are less abundant and individually

smaller than the millipedes, and for both of these reasons of less importance. More empty snail shells were found than of live snails, and the remains of slugs and sowbugs were not noted merely because of their rapid disintegration, and not because they served as a valuable source of food to any other animal.

In proportion to their size and abundance, the other plant and animal scavenger forms make no greater impression on their environment by what they eat than do the millipedes, sowbugs and snails, and then only by eating living tissue, a departure from their normal habits. But many of them do furnish an acceptable food for birds, and because of their habits; the method of eating and locomotion by earthworms, and of nest-building by ants, they effect considerable changes in the texture and humus distribution of the soil.

The phytophagous animals, even those of very unequal size and abundance, have a disproportionate rank depending upon the importance to the plant of the part of it on which they feed. A mere loss of some of its foliage is of minor importance to the plant. But a few small insects feeding on or burrowing into the tap root of a plant are more likely to promptly eliminate it than many larger insects feeding on the leaves. The larvae of midges or small beetles feeding on the ovaries and seeds may do more to restrict its future spread than much larger insects feeding on vegetative portions of the plant. As a source of food for other animals, however, the small insects are of importance only in proportion to their size.

Of greatest importance are the animals which are in large part or wholly predaceous, or parasitic on other animals. The minute egg-parasites, so small as to have been entirely unperceived in the present investigation, outrank, because of their effect on their hosts, the larger parasites which attack the more mature stages, although as a source of food for other animals they are negligible.

Many animals have a wide range in food, which broadens the variety of their relations to their environment, but decreases their specific importance to any particular element in their diet, and also renders more difficult their classification and assigning to groups based on feeding habits. Averages of what such animals eat over a wide range of environments may have but little value in indicating what the particular individuals concerned did eat in the region under observation, and in each case this must be determined from the place in which they were found and the food available there for their consumption.

THE AMOUNT OF FOOD EATEN BY INSECTS

Even the simplest individual problem of the absolute importance of one insect that feeds exclusively on a single host is far from being solved. Trouvelot (35) found that the caterpillar *Telea polyphemus* Cramer "when

56 days old—is fully grown and has consumed not less than 120 oak leaves, weighing three-fourths of a pound; besides this it drank not less than ½ oz. of water. So the food taken by a single silk worm in 56 days equals in weight 86,000 times the primitive weight of the worm (1-20th grain). Of this, about 1-4th lb. becomes excrementitious matter, 207 grains are assimilated and over 5 oz. have evaporated." The amount of corn leaves eaten by the armyworm, *Cirphis unipuncta* Haworth, has been measured in square inches (12), and the amount of clover leaves eaten by the weevil, *Hypera punctata* F. (34).

To obtain more complete data on various phases of insect growth, the tobacco hornworm, *Phlegethontius jamaicensis* Butler, was chosen because of its large size and rapidity of development. Hornworm eggs weigh .00105 gram each, and the just hatched larvae .0004 gram. The caterpillars were kept in small glass dishes with tight-fitting ground glass covers, the size of the dish being increased as the caterpillar grew and needed more room. The food of the caterpillars while in the first instar was not weighed, as the amount eaten was so minute, but the larvae were weighed daily, and their food and excrement in succeeding larval instars.

The figures on daily consumption of food and gain in net weight are not comparable, as the larvae might re-commence eating after molting at

TABLE 34. The Growth of Hornworm Caterpillars.

Instar	Days	Food Consumed:		Gain in Weight:				Excrement (Grams)	Percent of Food
		Weight in Grams	Percent of total	Grams	Percent of total	Percent Increase	Percent of food		
1st	3	.0208 gr.	.1	.0071 gr.	.2	1750	34.2*	.....	....
Larva 2nd	4	.0732	.4	.0285	.9	406	38.9	.....	....
"A" 3d	5	.4994	2.7	.1448	3.4	508	28.9	.....	....
4th	5	1.62	8.7	.5948	13.9	411	36.7	.7446	45.9
5th	7(1)	16.0367	86.6	3.4967	81.9	588	21.8	10.0032	62.4
Total	24	18.2501 gr.		4.2732 gr.		10733	23.4	10.7478 plus	59.-
1st	4	.0187 gr.	.08	.0064 gr.	.1	1600	34.2*	.....	....
Larva 2nd	6	.0788	.6	.0277	.5	432	34.9	.....	....
"B" 3d	5	.4067	1.7	.1359	2.7	490	33.4	.1176	28.9
4th	5	2.7756	12.	.8764	17.6	645	31.5	1.5908	57.3
5th	7	19.6591	85.6	3.934	78.9	448	20.0	12.5224	63.7
Total	27	22.9389 gr.		4.9818 gr.		12455	21.7	14.2308 plus	61.8
1st	4	.017 gr.	.07	.0058 gr.	.1	1450	34.2*	.....	....
Larva 2nd	4	.0478	.6	.0482	.8	831	32.6	.0232	15.7
"C" 3d	4	.3334	1.3	.1146	1.9	238	43.3	.091	27.2
4th	5	2.7845	10.9	1.0188	16.7	889	36.5	1.3612	48.8
5th	9(1)	22.1636	87.1	4.9203	80.6	483	22.2	12.9584	58.4
Total	26	25.4461 gr.		6.1077 gr.		15269	24.	14.4338	56.7

*Computed: average of 2nd, 3d and 4th of all three larvae.
(1) Days to attain maximum weight, not to end of instar or pupation.

any time of day or night. But in general, they showed enormous consumption of food relative to the weight of the larva in the first or first two days of the instar, but actually larger consumption of food in the last day previous to the pre-molting period because of the increased size of the larva. The apparent gain in weight was also greater in the first day or days of each instar because of partly digested food with which the alimentary canal was filled, and there was an apparent loss in weight in the pre-molting period as the digestive tract was emptied. But each instar represents a very definite period of growth, of which the net gain can be readily determined. Of the food consumed, between a fourth and a fifth became caterpillar, and nearly two-thirds excrement. Both fresh tobacco leaves and fresh excrement contain about 86% water (oven-dry leaves are 14.2% of their fresh weight and oven-dry excrement 14.01%) and presumably the caterpillars contained as high a percentage of moisture; thus the figures on fresh leaves, living caterpillars and moist excrement are about the same in relation to each other as those of oven-dry material. The data on excrement appear to show decreasing digestibility of the food as the caterpillars increase in size, and the last pellets excreted before pupation are lighter in color and possibly not as thoroughly digested as the others. But, aside from this, it actually indicates a partial drying-out of the excrement in the earlier instars because of the proportionately larger container used for the caterpillars when they were small. An average of the figures for the excrement of the 4th and 5th instars (54% of the weight of the food consumed) is probably approximately correct for the entire larval period. The smaller net gain of the caterpillar from the food consumed in the last instar is due to the physiologic changes occurring in preparation for pupation and not to a difference in the digestibility of the food. These physiologic changes and the ordinary muscular activities of the caterpillar entail the production of urates and other waste products. In addition to the undigested food, the pellets of excrement contain these waste products, which correspond to the urine in higher animals. As these two constituents of the excrement can not be mechanically separated, the presence of the urates adds another factor of error in the data on the excrement. It is however, a relatively constant element for most non-active caterpillars, and will increase considerably in amount in the last instar. The digestibility of, or rather the net returns from tobacco leaves by the hornworm caterpillars is around 40%, most of which becomes caterpillar in the earlier instars, but nearly half of which is used in internal changes in the final larval instar.

The data on maximum net gain are not as accurate as might be wished, for the weighing should be made as soon as the last pellet of excrement is eliminated, and not at the convenience of the experimenter, as the daily loss in weight after the maximum is reached, at least in the fifth instar,

amounts to about a third of the live weight, and as is later shown, the pupa weighs scarcely half the maximum of the larva. The remaining difference between food and caterpillar plus excrement is accounted for as losses of respiration of CO_2 and H_2O from the caterpillar, and from the leaf after weighing before it is consumed. Fresh tobacco leaves lost 20 to 25% of their weight the first day kept in tightly-covered glass containers, and the caterpillars never obtained all of the moisture they are credited with. There is also a loss of from 1 to 3% at each molt, the weight of the cast skin, and possibly an even greater, but incalculable, loss in the molting fluid.

For comparison with vertebrates which develop rapidly, the pounds of dry matter per day for each one hundred pounds of live weight of chickens and ducks, given by Mr. Wm. P. Wheeler (in 19, pp. 393-395) is as shown in Table 35.

TABLE 35. Ratio between Weight of Food and Live Weight of Animal.

	Chickens	Ducks	Hornworm Caterpillars
First two weeks....	10.1	17.2	20 (first four instars)
Two to four weeks.	9.6	17.0	46 (fifth instar)

The large consumption of food in the last instar of the caterpillar is for the internal activities and changes, and for maintenance until the adult can obtain food, as well as for growth. Nevertheless, it seems surprising that a sluggish, cold-blooded insect should consume so much more than active birds which have a high body temperature to maintain, even though the birds are able to digest, on the average, twice as much of their food.

The caterpillar of *Phegethontius jamaicensis* attains in 26 days, 12,486 times its original weight (1-2500 gram) and has eaten an amount of food 55,600 times its primitive weight: that is, in half the time required by *Telea polyphemus* it attains more than three times the relative weight of the latter and consumes nearly one-third less food. The difference is due to many factors, the most obvious being the difference in weight of the just-hatched larva, 1-2500 gram for the hornworm and 1-20th gram for the silk-worm, really a most unfortunate selection as a basis for comparison. Actually, however, the data carried thus far mean practically nothing, as the fully grown caterpillar is not an adult insect; it has merely attained its maximum growth.

Of the three caterpillars, one, "A", escaped when fully grown and lost its life in a battle with a lizard. The other two were reared to adult, and from them the data given in Table 36 were obtained:

The pupae were not weighed daily as it was feared that the incidental disturbance might prevent the emergence of the adults. The loss of H_2O from the pupae was possibly abnormal, as they were not buried in moist soil, but kept in a closed glass container. The meconium, which consists of the non-gaseous by-products of the activities of the insect since the first day after it, as a fully-grown caterpillar, ceased voiding excrement, is excreted by the moth immediately on emergence and was so scattered that it could not be weighed to separate it from the loss of water experiencd by the moth in expanding and drying its wings, and the combined weight of these factors is obtained by difference between pupa and adult plus pupal skin.

TABLE 36. Food Eaten by Hornworm Caterpillar compared with Pupa and Adult.

	"B"	"C"
Weight of pupa, February 2	2.541 gr.	3.0895 gr.
Weight of pupa, February 13	2.3155 gr.	2.8542 gr.
Percent of daily loss	.842%	.672%
Computed weight of pupa at beginning	2.648 gr.	3.1965 gr.
Computed weight of pupa at end	2.1443 gr.	2.7044 gr.
Weight of pupal skin	.0346 gr.	.0344 gr.
Computed weight of meconium and H_2O loss	1.4105 gr.	1.6518 gr.
Weight of food eaten by larva	23.02 gr.	25.447 gr.
Live weight of adult	.6992 gr.	1.0182 gr.
Percent of weight of food eaten by larva	3.02%	4.001%
Oven-dry weight of food eaten by larva	3.225 gr.	3.565 gr.
Oven-dry weight of adult	.277 gr.	.399 gr.
Percent of weight of food eaten by larva	8.6%	11.2%
Ratio: weight of adult to food eaten by larva	1: 11.6 a male	1: 8.9 a female

The computed maximum oven-dry weight of the larva is 2.15 times (2.15 for "B", 2.14 for "C") that of the adult; that is, the insect loses over half its dry weight in transforming from larva to adult. The final data showing that the oven-dry moth weighed approximately one-tenth of the oven-dry weight of the food consumed by the larvae, are only an approximation for the species, but even for only two individuals gives a basis for comparison with other insects.

Mr. J. J. Davis has very kindly furnished the air-dry weight of adults of *Cirphis unipuncta* (10 museum specimens) as being approximately .048 plus grams. Ten weighed .48 gr., five weighed .235 gr. The air-dry weight of corn leaves from young plants is .02108 gr. per square inch, and .0311 gr. for leaves from mature plants, of which the armyworms ate 41.4 square inches to complete their development, or from .872712 gr. to 1.28754 gr. The adult weighs from 5.5%, or 1-18th, to 4.-% or 1-26th of this. Its larval period (26 1-2 days) averaged one-sixth less than the hornworm, and obviously corn leaves are less nutritious for armyworms than tobacco leaves

for hornworms. Indeed, the results computed from Mr. Davis' data are so far removed from those on the tobacco hornworm that it seemed desirable to determine how great are the variations in the amount of food eaten by caterpillars on different and the same host plants.

In most of the feeding experiments which were later conducted, only the last and the next to the last instars of caterpillars were used, the amount of food consumed in the earlier instars, small in any case, being readily compiled from that eaten in the next to the last larval instar. The excrement and the portions of the uneaten leaf were dried before weighing, to eliminate the error due to partial drying out which appeared in the hornworm experiment. Several larvae of *Felita annexa* Treitsche, a common cutworm of tobacco in Porto Rico (where these later experiments were conducted), were used in the first experiment, but only one transformed to adult under the abnormal conditions involved.

TABLE 37. Food eaten by Cutworm compared with Its Weight.

Maximum gross weight of larvae	Weight of food eaten while under observation		Excrement: dry weight	Digestibility of food
	Fresh	Dry		
1. .807 gr.	3.891 gr.	.551522 gr.	.175 gr.	60%
2. .767 gr.	4.517 gr.	.641414 gr.	.253 gr.	60%
3. .642 gr.	5.582 gr.	.792644 gr.	.361 gr.	55%
4. .37 gr. (died)				

Larva number 3 transformed to an adult which weighed (dry) .064 gr. Its larva had eaten 3.746 gr. of fresh tobacco leaves, or .5244 gr., dry, or 8.2 times as much as the weight of the adult.

A larva of *Prodenia ornithogalli* Guenee, another tobacco cutworm of Porto Rico, which attained a maximum live weight 1.7 gr., ate 6.697 gr. (5.6253 gr. weighed and 1.0717 gr. computed) of fresh tobacco leaves, or .93758 gr. dry, but died in pupating. Other adults (air-dry) weigh about .1 gr., so its relation to food eaten is probably very much the same as of *Feltia*. Also, an approximately equal portion of the food which it ate was transformed into insect, 55%, as of the 5.6253 gr. of food weighed out to it, .36 gr. of dry excrement was obtained. The two cutworms are able to digest and assimilate 55 to 60% of the tobacco leaves and produce adults weighing a little more than one-tenth as much as the food they ate. The hornworm caterpillars, which were able to digest only a little more than 40% of the tobacco leaves, nevertheless produced adults which weighed about one-tenth of the food they ate.

A fresh cotton leaf was given to three larvae of *Alabama argillacea* Hübner which had just molted to the last instar. In three days they had consumed practically all of it and spun cocoons to pupate. The amount

actually eaten, after the weight of the stem and fragments had been subtracted, equalled 4.0488 gr., or dry .971712 gr. The total net weight of the caterpillars at the beginning of the instar was .2436 gr., and at the end .816 gr., a gain of .5724 gr., or 235%, but this is only 14.1% of the weight of the food eaten. The dry excrement weighed .6448 gr., thus the digestibility of the cotton leaf by these caterpillars is less than that of tobacco, or only 34.7%. The hornworms gained approximately 80% of their weight in the last instar, but ate 85% of their food at this time. The *Alabama* caterpillars gained 70% of their weight in the last instar, and may be presumed to have eaten about 75% of their food in this instar. On this basis, the total food eaten amounted to 1.3 gr. (dry weight) to produce three moths whose dry weight was .1025 gr., giving a ratio of moth to food of 1 to 12.6. The lower digestibility of the cotton leaf by the *Alabama* caterpillars naturally results in a greater amount of it being required to produce a proportionate amount of insect.

A larva of *Laphygma frugiperda* Smith & Abbot was able to digest only 25% of tender corn leaves with which it was fed, and the adult (dry) weighed one-twentieth of the dry weight of the food that the larva had eaten. Comparing these data with the results Mr. Davis obtained with the armyworms, which were also fed on corn, it would appear that substantially similar insects feeding on the same host require relatively the same amount of food to produce adults.

More extensive experiments with fifteen larvae of *Xylomiges eridania* Cramer, and ten larvae of *Bombyx mori* F., fed on mulberry leaves, with food and larvae weighed after the first instar, give somewhat similar results. The caterpillars of the Noctuid digested 36% of the somewhat dry and fibrous leaves of *Morus tartarica*, and ate 26.4 times as much food as their adults weighed. The silkworms digested 41% of the tender leaves of *Morus alba*, and ate 23.8 times as much food as their adults weighed. The cocoons produced by the ten caterpillars, weighed 9.702 gr., of which the silk was 1.1195 gr., or 4.2% of the weight of the food eaten. The weight of the moths (air-dry) was .601 gr., and of 1392 eggs (computed from that of unhatched eggs of the previous generation) .599 gr., a total of 1.1 gr., for both adults and eggs, or not as much as the weight of the silk. The digestibility of the mulberry leaves by the caterpillars was greater than that of cotton and corn, but considerably more of them were eaten to produce adult moths. Apparently it is true in only a rather general way that the amount of food required by insects is inversely proportional to its digestibility.

In Table 38, the air-dry weight of the food of some insects is compared with the weight of the adult, and the ratio between them given. None of these data is as accurate as might be desired, as the weight of all the insects is plus the weight of food and excrement in the alimentary canal, and is not

net as was that of the hornworm and some of the other caterpillars. An additional source of error is that in the case of the parasitic insects which suck the juices from their prey, the weight of the chitinous exoskeleton of the host, which, strictly speaking, is not eaten, has not been subtracted from the weights given, and this would give in some cases a much lower ratio than is indicated. Thus, predaceous insects, which swallow their prey instead of sucking the juice out of it, presumably have about the same ratio as is given for the parasites in the above table. The phytophagous insects also have about the same ratio when the food is leguminous, in which case it forms a concentrated balanced ration, the crude fiber of the plants ingested being the equivalent of the indigestible chitin eaten by the predaceous insects. The amount

TABLE 38. The Amount of Food required to Produce an Adult Insect.

Insect	Weight in grams	Food or Host	Its weight in grams	Ratio
Hypera punctata F., the clover-leaf weevil	.01552	3.09 sq. in. of clover leaves (34)	.10297	1: 7
Bruchus dominicanus Jekel, a bean weevil	.00312	beans of *Acacia farnesiana*	.02294	1: 7.38
Tiphia transversa Say a Scoliid wasp	.024	*Lachnosterna* white grubs	.27325	1: 9
Tiphia spp., Scoliid wasps, females	.0276			
Campsomeris dorsata F., a Scoliid wasp, male	.039	grubs of *Ligyrus tumulosus* Burm.	.28	1: 7
female	.046			1: 6
Elis haemorrhoidalis F., a Scoliid wasp, male	.006	grubs of *Phytalus apicalis* Blanchard	.03562	1: 6
female	.013			1: 3.-
Pyrgota undata Wied., a parasitic fly	.222	*Lacnosterna dubia* Smith	.21	1: 9
		Lachnosterna fusca Froelich (May beetles)	.17	1: 8
Ophion bilineatus Say, an Ichneumonid wasp	.019	larvae of *Feltia venerabilis* Walker	.1178	1: 6.2

of protein is much less in non-leguminous plants, thus a much greater amount of such food must be consumed by the insects. The cell-sap of some plants may form a perfectly balanced ration for some insects, as is indicated by the fact that the excreta of the leafhopper, *Kolla similis* Walker, even when feeding on the young shoots of sugar-cane is clear, colorless, tasteless and devoid of sugar. Such an almost perfect consumption by the insect of the plant juices on which it feeds is due to its active habits. By contrast, the scale produced by scale-insects and the honey-dew excreted by aphids and mealybugs is an excess of carbohydrates which can not be assimilated by these sedentary or sluggish insects because of their rapid growth and lack of muscular activity.

Animal and plant juices may be almost entirely and completely assimilated by most of the insects feeding on them, and they undoubtedly furnish food in its most digestible form. But even crude fiber can be assimilated by the digestive apparatus of the animals which feed upon it. The decaying plant tissue eaten by snails, slugs, millipedes and sowbugs, and the dung in-

habited by some of these animals and Elaterid and Threviid larvae can be digested by them. One thinks of wood as being almost entirely cellulose, and quite undigestible, yet the dry-wood termite, *Cryptotermes brevis* Walker, can assimilate over half of the wood of Sitka spruce eaten by it (40). Of other, less preferred woods, it assimilates smaller portions, but this only further serves to illustrate the point that the digestive apparatus of animals is usually well adapted to digest the food which they prefer.

The consumption of food by an organism has these purposes: (1) maintenance, (2) growth, (3) reproduction and (4) storage for any of the other three. Some insects concentrate the consumption of food for all of these purposes into the larval period, while many continue to eat (usually different kinds of food) when adult for maintenance and reproduction, but for practically all, growth is confined to the larval period. In a general way it is known that of the warm-blooded animals, those maturing most rapidly obtain a greater adult weight for the food consumed than those which mature more slowly, and the smaller animals require more for maintenance in proportion to their size than do larger animals. Cold-blooded animals require food for maintenance only in proportion to their size and activity, but like the warm-blooded, inversely in proportion to their rate of growth. It is obvious that insects which develop slowly, which even in the tropics with continually favorable temperatures require an entire year for their life-cycle, and in the temperate zone require three to five years, such as white grubs and wireworms, eat less per day in proportion to their size, but certainly consume more for maintenance because they live so long. Active insects with a rapid development, like grasshoppers and leafhoppers, eat most per day, but make a less advantageous use of their food for growth than do other insects with about the same rapidity of development that remain quiet and consume less energy in voluntary activity, such as aphids and caterpillars. Insects which develop wings and heavy chitinization, and with a complete metamorphosis in their development, require more food for these structures and for the changes and losses involved in passing through the pupal period, especially when this is protected by an extensive silken cocoon. The cocoons of *Tiphia* and *Bombyx* weigh somewhat more than do the (air-dry) adults, and that of *Ophion* twice as much.

Two of the factors involved in the most economical use of foods for growth by insects have to do with the food: (1) the closeness with which it approximates being a ballanced ration for supplying the needs of the insect, and (2) its digestibility. The others have to do with the insect, its rapidity of development, the amount of its activity, and the production of wings, silk, scales, wax, heavy chitinization and similar structures.

Honey-dew and the nectar of flowers, although not used for growth, are admirably adapted to the needs of adult insects with a high rate of muscular activity, such as butterflies, moths, flies, bees, wasps and ants. All of these

insects in their larval stage, no matter what their food may have been, primarily required from it the proteids which are essential for growth. But as adults, carbohydrates, especially if in solution and readily available for assimilation, much better meet their needs. Insects, such as most phytophagous and scavenger beetles which are not especially active as adults, may continue to eat the same kind of food that was acceptable to them as larvae, for the usually small proteid content of their food is now essential for reproduction. Most of the predaceous insects, such as dragon flies and the Carabid and Cicindellid beetles, are as active as any of those feeding on the almost pure carbohydrates, but swift mobility to capture their prey is essential, and is maintained despite (and not because of) the high proteid content of their food.

Many insects normally live for a long time as adults, the eggs of the female not maturing for several weeks or months after the emergence of the adult from the pupal stage. Such insects may consume more food for maintenance as adults, and especially for reproduction, than they did as larvae for growth. The clover-leaf weevil as an adult eats 4.76 square inches of leaves and "at least an equal amount of stem" (34) for maintenance, aestivation and reproduction, as compared with 3.09 square inches of leaves eaten by the larva for growth and maintenance. An Otiorhynchid beetle, *Prepodes roseipes* Chevrolat, feeding on the leaves of sea-grape, *Coccoloba uvifera*, which have a digestibility of 42.6% for this beetle, ate .399 gr. of fresh leaf in four days, or about the equivalent of its own weight, .0982 gr., per day. Such beetles often live for two or three months, and in the course of their life eat a tremendous amount of their host, in proportion to their size. Most of this food is transformed into eggs, which weigh several times as much as does the female producing them. Thus, the composition of the food, the length and activity of the life of the adult, the number and size of the eggs laid by the female all affect the amount of food which is consumed by the adult.

The amount of food required by an animal for growth, maintenance and reproduction varies so greatly, and depends on such a large number of factors, that for exact results it must be determined by direct measurement with individuals of the species concerned. Much more work of this kind must be done before one can safely generalize, but for the necessities of this census, it will be considered that the following classes of animals require approximately the amounts of dry weight of food multiplied by their own dry weight as indicated in Table 39.

But even when the kind and amount of food eaten by an individual insect and the number of these insects present is known, this does not give all the essential factors necessary to determine the amount of food eaten by the species. The predators and parasites of it are the unknown factor.

They may gradually and quite evenly reduce the number of certain kinds of insects so that the product of their abundance by weight remains constant. Or the majority of the individuals of a species may be able to attain full growth before being killed by their enemies. Also, the average abundance of an insect throughout the season from April to October, seldom indicates its importance during the few weeks of its maximum activity. Each insect is a special case, and in the discussion which follows, the abundance per square foot used in the computations covers only the period of its activity, either as caterpillar for the Lepidoptera or as larva or nymph and the first few weeks of maximum abundance of adults for the other insects. Thus, it does not include the food consumed by the stragglers at either end, when the species was not at its period of maximum activity, and the figures to be given are in reality underestimates. For comparison with what the insects eat, a digression is here necessary, however, to determine what the other animals present in the grasslands ate, quantitatively and qualitatively.

TABLE 39. Food Requirements of Insects.

Group of Insects	For GROWTH, as larvae of nymphs	For MAINTENANCE and REPRODUCTION, as adults
Lepidoptera and Cleoptera feeding on grass or other non-leguminous plant tissue	20	30 (Coleoptera)
Lepidoptera and Coleoptera feeding on leguminous plant tissue	7	10 (Coleoptera)
Grasshoppers (mostly grass feeders)	15	15
Crickets (mixed feeders)	10	10
Predaceous Insects and Ants	8	15
Aphids and Mealybugs	7	15 (aphids only)
Leafhoppers and other active sucking insects	5	10
Spiders	5	10
Parasitic Insects	5 (or less)	

THE AMOUNT OF FOOD EATEN BY BIRDS

Chickens assimilate about 80% of the dry weight of the food they eat. From data given by Mr. Lippincott (20) and Mr. Slocum (32 & 33), it appears that Barred Plymouth Rock pullets, of which the standard live weight is six pounds (or 3.3 lbs., dry weight) consumed thirty pounds of dry matter in attaining their growth to maturity (egg-laying), or 9.09 times their dry weight. Hens of the same breed, averaging 144 eggs, consumed in a year 22 times their own dry weight, and White Leghorn pullets, averaging 135 eggs, 30 times their own dry weight in the same period. No careful or extensive quantitative data are available for any wild birds, and the data on chickens can serve as only the basis for a rather doubtful comparison on

how much robins and other birds present in the grasslands might be expected to eat. As young robins develop more rapidly than chickens, they consume more proportionately per day, and after attaining maturity and leaving the nest, they are more active and presumably require more for maintenance than do chickens. Although as adult the female robin lays fewer eggs, she requires more food for flight and for collecting food for herself and young. Ten times the adult's weight of food to attain maturity, and fifteen times for maintenance and reproduction for six months, from mid-April to mid-October, are certainly most conservative estimates of the food consumption of the wild birds, and the amounts actually eaten may easily be two or three times as much.

THE ANIMAL FOOD AVAILABLE FOR THE BIRDS TO EAT

Table 40, on the dry-weight of insects in pounds per acre in the meadow and pastures at Barneveld, is primarily to show the amount of food available for the insectivorous birds for the six months mid-April to mid-October, and it should not be interpreted as giving the weight of any specific insect at any particular time. The data are not accurate for a number of reasons. When possible, ten or more adults of each species were weighed, but in many cases, only one or a few specimens were available. The weights of the more important are quite exact, and that of the grasshoppers represent the weighted average of all the species collected, but for some groups containing large numbers of unidentified forms, the estimates may be a considerable departure from the actuality. This is especially true of "other Lepidoptera" and "other Diptera". No estimate of the weight of the very small insects is given, as they are not a source of food for the meadow and pasture birds. In all cases, except for the insects with an incomplete metamorphosis, the adult weight has been used in the computation. The weight of the larva in the last instar for such insects is at least twice as great as that of the adult, so the adult weight has been arbitrarily taken for an average of the weights of all stages normally available for bird food. For the insects with an incomplete metamorphosis, the Orthoptera, Hemiptera and Homoptera, which attain their maximum weight as adults, *half* the weight of the adult has been taken for an average of the motile stages.

This table brings into more striking relief the insects important as a source of food to the birds because of their size or abundance, or both: the grasshoppers and crickets, the *Acucephalus* leafhoppers, the cutworms, the Carabid and Elaterid beetles, the May beetles and white grubs, *Phaedon aeruginosus*, *Hypera punctata* and other Curculionid weevils, and the ants.

(In the pasture of scant vegetation, where the cows average one per three acres, the dry weight of cow per acre for the 14 hours spent there is about 165 pounds, or over six times as much as the dry weight of the in-

TABLE 40. The Amount of Insect Food Available for Birds to Eat in the Grasslands at Barneveld, New York.

Insect or Group of Insects	Dry Weight of One Individual in GRAMS	Dry Weight in POUNDS per Acre of:		
		Meadow	Scant Pasture	Abundant Pasture
all grasshoppers	.0422 gr.	1.36 lbs.	.65	2.9638 lbs.
Gryllus assimilis (cricket)	.07	.97	.8	3.65
Nemobius fasciatus (cricket)	.025	.418	.576	3.0605
Total Orthoptera		2.748	2.026	9.6743
Sinea diadema (bug)	.021	.02	....	.....
Nabis spp. (bugs)	.015	.04	.165	.1944
Miridae (Capsid bugs)	.006	.092	.069	.063
Geocoris uliginosus	.0006	.02	.01	.0085
large Hemiptera	.02	.17	.195	.15
Total Hemiptera		.0342	.439	.4159
Acucephalus spp.	.00288	.55	.57	1.488
all other leafhoppers	.001	.235	.115	.155
Membracidae (treehoppers)	.002	.025	....	.07
Cercopidae (froghoppers)	.0012	.038	.0325	.025
Total Homoptera		.848	.7175	1.738
Cutworms (Noctuidae)	.0415	1.47	4.38	2.6
other Lepidoptera	.01	.85	.76	1.32
Total Lepidoptera		2.32	5.14	3.92
Predaceous Diptera	.005	.115	.29	.2
Pacharhina ferruginea	.03	.01	.75	.8
other Diptera	.0095	.06	.05	.08
Total Diptera		.275	1.09	1.08
large Carabidae	.025	.48	.24	1.728
Staphylinidae	.001	.1	.1	.17
Coccinellidae (lady-beetles)	.0018	.025	.01	.02
Histeridae	.011	.08	.06	.....
Elateridae (wireworms)	.027	.7776	3.1104	2.928
Telephoridae (fire-flies)	.011	.2	.37	.23
Onthophagus hecate	.011	....	.16	.....
Aphodius fimetarius	.014	.1244	.1244	.....
Lachnosterna spp. (grub .27)	.2	3.456	8.064	3.2
Phaedon aeruginosus	.00188	.10288	.1101	1.29404
other Chrysomelidae	.0022	.02	.27	.29
Hypera punctata	.01552	.15	1.74	1.
other Curculionidae	.00155	.65	.75	.72
Total Coleoptera		6.16588	15.1089	11.58004
all Ants	.001	1.312	2.56	1.3806
Ophion bilineatus	.019	.11	.18	.09
Bees	.0024	.0092	.046	.....
Total Hymenoptera		1.4312	2.786	1.47
Total INSECTS		14.13	27.3075	29.8782

sects living there. In the pasture of abundant vegetation, where the cows average one per eight acres, the dry weight of cow per acre for the 8 hours of each day they spend there is 62.5 pounds, or twice the weight of the insects living there. If to this is added the weight of the other invertebrates, the earthworms, millipedes, sowbugs, spiders and snails, and that of the smaller vertebrates present in this pasture, the total weight of wild life might amount to nearly as much as that of the domestic animals.)

The robins constituted such a large part of the bird life of the meadow-pasture area that a comparison of the food they normally eat with what there was present for them to eat in this area will show whether or not they discriminate for or against any particular insect or class of insects. Prof. S. A. Forbes (14) has given a very careful qualitative and quantitative record of the food of the robin in central Illinois for nine months, February to October. Sixty-five percent of the robin's food is insects, and from this the 15 percent of Bibionid larvae, eaten almost entirely in February and March, and not present in the grasslands at Barneveld, may be subtracted, so that Prof. Forbes' figures have been doubled to give approximately the percent of insect food eaten for the period April to October. In further explanation, it should be noted that at the time of his investigations (1880 or earlier), *Hypera punctata* was not present in Illinois, although now it forms an important item in the robin's diet. Also, *Phaedon aeruginosus* is presumably not present in Illinois.

TABLE 41. Comparison of the Insect Food Known to be Eaten by the Robin in Illinois from April to October, and the Amount of Such Food, expressed in percentage by weight of the total amount, Present in the Pastures and Meadow at Barneveld, New York.

Insect, or Group of Insects	Eaten in Illinois	Present at Barnveld in:		
		Scant Pasture	Abundant Pasture	Meadow
Grasshoppers	6.%	2.57%	11.52%	10.92%
Crickets	2.	5.44	26.04	11.1
Pentatomids	4.	.77	.58	1.3
Noctuid larvae	16.	17.32	10.105	11.8
Other Lepid. larvae	18.	3.	5.13	6.82–
Tipulidae	2.	2.97	3.11	.1
Carabidae	10.	.95	6.71	3.85–
Histeridae	2.	.23	....	.7
Elateridae	4.	12.29	11.37	6.23
Lampyridae	1.	1.46	.81	1.6
Lachnosterna	6.	31.88	12.43	27.69
Other Scarabaeidae	8.	1.12	....	1. –
Curculionidae	4.	9.88	6.68	7.4
Ants	8.	10.12	5.36	10.5

By combining such similar items as grasshoppers and crickets, Noctuid and other Lepidopterous larvae, *Lachnosterna* and other Scarabaeidae, the columns are found to be surprisingly similar; that of the pasture of scant

vegetation, the preferred environment for the robins at Barneveld, most closely approximating the Illinois records. The most striking differences are in the Carabids, of which the Illinois robins ate ten times as many as of the other insects present in the pasture at Barneveld, although these beetles are no more abundant in Illinois than in New York State. It appears quite probable that the reason why they were so scarce in the preferred environment was because the robins had eaten most of them. Of the Histerids also the robins had eaten many more than were available at Barneveld, and, in proportion to the other insects, only a third as many Elaterids as were present in the New York pastures. Thus, except for its specialties of Carabid and Histerid beetles, the robin eats for the insect part of its food everything of reasonable size that is present in the closely-grazed pastures which are its preferred hunting grounds for obtaining such food.

The live weight of the adult robin is about three ounces (or 1.5 oz. dry weight), and if each adult eats fifteen times its dry weight of food in six months, this amounts to a pound and a half, or of insects alone (65%) about one pound. Even where the robins are most abundant, in the pasture of scant vegetation averaging two per acre, this constitutes less than one-twenty-fifth of the total weight of insects present. But if each pair raises two broods of five young to maturity, each of which eats ten times its own adult weight of food, they constitute a by no means insignificant factor, and on the insects for which they show a decided preference they levy a heavy toll. Their consumption of Carabid beetles, which constituted ten percent of their insect food in Illinois, amounts to one-tenth of a pound per bird. On this theoretical basis, they would have eaten one-fifth of a pound of Carabids in the pasture of scant vegetation, and only one-fourth of a pound of these beetles was present there, as compared with half a pound present in the meadow and a pound and three-quarters in the other pasture, where the robins were less abundant. Indeed, it seems obvious that the numbers of these beetles, and of robins, are inversely proportional.

As compared with some other birds, robins eat few ants, but their 8% of ants amounts to one-fifteenth of all present. Ants constitute three-fourths of the food of flickers, and as they are larger birds than robins, they eat considerably more than ten times as many ants as do robins. If they were as abundant as the robins, they would soon eliminate their principal source of food. The common birds sometimes show a surprisingly great variation in specific abundance depending on apparently slight differences in environment, but on more careful examination of the environment as a source of food, their numbers will be found to be closely correlated with abundance of food. The large number of robins in the pasture of scant vegetation was not an accident, but primarily due to an abundance of the insects which form their staple food, coupled with comparative ease of obtaining it due to the shortness of the turf.

WHAT THE FARMER OBTAINS FROM PASTURE AND MEADOW

Having noted what and how much the birds and insects ate in the pastures and meadow, a consideration of how much the cows ate in the pastures and how much hay was cut in the meadow is essential for comparison.

The difference in the amount of food required for keeping a cow during the six winter months, as compared with that of the six summer months, due to the food obtained from the pasture, when converted into its equivalent of fresh clover and grasses amounts to 13,400 pounds (2). This amount of fresh forage should be obtained from three acres of pasture by each cow in six months, and is the equivalent of 4,025 pounds, or about two tons, of hay made from clover and grasses with 10% moisture. At Barneveld, the two pastures furnished pasturage for nine cattle, which consumed 36,205 pounds (air-dry weight) of pasturage in the 22 hours daily of the summer when they were out of the barns, or 1,600 pounds per six month-hour. They spent fourteen hours daily in the fifteen acre pasture of scant vegetation and ate 1,300 pounds of pasturage here. In the twenty-five acres of the pasture of abundant vegetation, they spent only eight hours daily, and ate only 512 pounds of pasturage per acre. The farmer who mowed the meadow claimed that it didn't yield one ton of hay to the acre, but he refused to be more specific, and no exact measurement was obtained.

The mowing machine is undiscriminating and harvests everything big enough to cut, and stock, unless overfed, will eat small amounts of almost any plant that happens to occur in the hay, except for the stems and coarse leaves of dock and some other large weeds. In the pasture, cows are more discriminating, as they have the whole field to choose from, but not all the forage the cows obtain from pastures is clover and grass, for they do not reject all the other plants present there. In the pastures at Barneveld, it was noted that the cows specifically avoided some plants, which are listed in Table 42. Whether cows will eat a given plant, or not, depends upon accident, the individual cow, how abundant the plant is, and how much there is to eat of other more desirable plants. But if, of tall plants at least, they stand out above the rest of the pasture, and if they have no difficulty in flowering, it is pretty certain that the cows do not ordinarily touch them. But most other plants are not specifically discriminated against, and their leaves and stems disappear with the grass and clover, especially if all are growing together. They should thus be credited with furnishing their proportionate share of the forage, even if their feeding value may be low. On this basis, white clover, for instance, does not constitute a third of what fodder the cows obtained in the pasture of scant vegetation, but less than one-sixth, or 220 pounds.

TABLE 42. Plants in the Pastures at Barneveld NOT Eaten by Cows.

Plant	Percent of ALL Vegetation in:	
	Scant Pasture	Abundant Pasture
Moss (Polytrichum spp.)	9.3	4.7
Sorrell	6.9	3.4
Buttercup	3.3	10.9
Canada Thistle	2.7	1.
Everlasting	2.	2.1
Lichens and *Cladonia*	1.4	.5
Ironweed	1.	.2
Bluets	.7	...
Yarrow	.5	.4
St. Johnswort	.2	...
Moth Mullein	...	.1
	28. %	23.3%

A COMPARISON OF THE AMOUNT EATEN BY COWS AND BY INSECTS OF SOME PLANTS: WHITE CLOVER

Multiplying by 96 the weight in grams of food consumed per square foot by any insect gives the weight of food in pounds per acre consumed by that insect. Five insects are known to have fed specifically and exclusively on white clover in the pasture of scant vegetation, and, as shown in Table 43, they ate 75.87 lbs., or one-third as much of it as the cows did.

TABLE 43. Consumption of White Clover by Insects.

Insect	Dry Weight of Adult	Ratio to Food	Dry Weight of Food	Insects per sq. ft.	Food, in lbs. per Acre
Feltia venerabilis larva	.0415 gr.	1:17	.2905 gr.	1.2	33.5 lbs.
Hypera punctata	.01552 gr.	1:17	.26384 gr.	1.44	36.3 lbs.
Sitona flavescens and *S. hispidula*	.00155 gr.	1:77	.02638 gr.	2.	5.0 lbs.
Agallia 4-punctata	.0005 gr.	1:15	.0075 gr.	1.5	1.07 lbs.
					75.87 lbs.

But there was a considerable number of other large insects present which ate some white clover, and because of their size and abundance, their share of the clover amounted to about a third of what the insects specifically feeding on it consumed. Like the cows, the grasshoppers, crickets, crane-fly larvae and white grubs do not specifically feed on any one kind of vegetation, but, so far as has been observed, eat whatever happens to be available. It is difficult to estimate at all accurately how much they do eat, because of their wide range of food and its differences in digestibility, and the problem is further complicated in the case of white grubs because of their slow development. But it seems a reasonable estimate that the amount of white clover consumed by the insects in this pasture, whether they ate it ex-

clusively, partially or only incidentally, amounts to at least half of what the cows ate.

In the pasture of abundant vegetation, the insects specifically feeding on white clover were less abundant, but the grasshoppers and crickets were much more abundant, while the cows were considerably less numerous, so much so indeed, that conservative estimates indicate that in this pasture, the insects ate MORE of the white clover than the cows did.

A COMPARISON OF THE AMOUNT EATEN BY COWS AND BY INSECTS OF SOME PLANTS: GRASS

In the pasture of abundant vegetation, two leafhoppers, *Acucephalus albifrons* and *Acucephalus striatus*, averaged in abundance fifteen per square foot and eighteen per square foot respectively during the months of June and July. The dry adult female of the former weighs .00228 gr., and if this represents one-fifth of the dry weight of the cell sap they consume in growth, then these two species sucked 36 pounds of plant nutrients from the grasses in this pasture in two months. During the same period, the cows ate 66 pounds of grass in this pasture (40%, for June and July, of the 1-4 ton per acre of all forage, of which one-third was grass), or an amount of nutrients LESS than what the leafhoppers obtained, as the digestibility of the whole grass by the cows is half of that of the cell-sap by the leafhoppers. The number of leafhoppers present decreased so sharply in early August that what all the adults consumed for maintenance and reproduction is less than a tenth of what the nymphs consumed for their development.

The crickets and grasshoppers in this pasture were abundant from the latter part of June to mid-September, decreasing in numbers as they grew in size, and thus maintaining a fairly constant total consumption of food. The dry weight of grasshoppers per acre in this pasture averaged throughout the season was 2.9638 pounds, but this figure includes the areas examined in the spring and late fall when few or none were present, and to obtain their abundance in the summer, should be doubled. If this represents thirty times what they ate during the life-cycle, this amounts to 177.828 pounds of vegetation. The crickets weigh 6.71 pounds, and, doubling this for mid-summer abundance, but multiplying only by twenty, as the crickets have a more varied and nutritious diet, their food weighs 268.4 pounds. The total food consumption by the Orthoptera for summer was 446.228 pounds. Even supposing that they ate no more proportionately of the grass, which was one-quarter of all vegetation, than of the other plants, this amounts to 111.6 pounds of grass.

The grass cutworm, *Nephelodes minians* (?), which during late June and early July averaged 1.3 per square foot, ate 106.3 pounds of grass during its

larval period. The Crambid caterpillars, earlier and later in the season, other miscellaneous grass-feeding caterpillars and the grass-feeding saw-fly larvae, *Dolerus* sp., possibly ate enough to bring this up to 150 pounds.

Of the quarter of a ton of forage which the cows ate in the pasture of abundant vegetation, one-third, or 166 pounds was grass. Combining the consumption of grass by all the various insects in this pasture which ate it exclusively, partially or only incidentally totals a little over twice as much as what the cows ate.

A COMPARISON OF THE AMOUNT EATEN BY COWS AND BY INSECTS IN TWO PASTURES

In the pasture of abundant vegetation, the most important insects in the consumption of forage which the cows might have eaten were not those which specifically fed on grass or clover, but those which fed omnivorously on all sorts of vegetation: grasshoppers, crickets, white grubs and crane-fly larvae. On the supposition that they ate no more of the weeds than they did of grass and clover, they prove to be the dominant factor in indicating a consumption by insects in this pasture of approximately twice as much grass and clover by insects as by cows.

In the pasture of scant vegetation, the cows ate very considerably more of the grasses and clover than did the insects, relatively because the insects were less abundant, and absolutely because they were there long enough and in sufficient abundance to eat most of the surplus vegetation. This kept the vegetation short, so that this pasture was a less attractive environment for crickets, grasshoppers and leafhoppers, and also it was more attractive to robins, who foraged there in greater numbers and thus further reduced the number, not only of Carabid and Histerid beetles, but of all large insects.

SURPLUS VEGETATION AND ITS DISPOSAL

If grass and other vegetation is not eaten by cows and phytophagous insects, it eventually becomes available for the plant scavengers, such as snails, slugs, sowbugs and millipedes. The small number of such animals found in the pasture of scant vegetation, which is further greatly reduced if those occurring in dung are subtracted, is an index of the completeness with which these plants were consumed as living tissue, while the large number present in the other pasture shows how much more surplus vegetation was present than could be utilized by the cows and insects. The greatest amount of decaying vegetation was present in the meadow, where there were fewer insects, and the single mowing did not begin to make up for the absence of cows.

TABLE 44. The Number of Plant Scavengers per Hundred Square Feet in the Grasslands at Barneveld, New York.

Animal	Meadow	Abundant Pasture	Scant Pasture
Slugs	34	16	6
Snails	182	43	6
Sowbugs	215	55	10
Millipedes	772	666 (5/6ths in cow dung)	352 (2/3ds in cow dung)
	1203	780	374

THE INSECTS OF THE MEADOW

In the meadow, there was no insect or group of destructive phytophagous insects to compare in importance with those found in pastures. Most of those found in the pastures are present in the meadow, if their host plant is present, but usually in smaller numbers. Less than half as many grasshoppers and a fifth as many crickets were present as in the pasture of abundant vegetation, and a half to a third as many cutworms as in the pastures, and half as many white grubs as in the pasture of scant vegetation. The insects feeding on the two distinctive meadow plants of economic importance, red clover and orchard grass, are for the most part insignificant in size and number.

Feeding rather specifically on orchard grass, 124 leafhoppers were noted: 87 *Xestocephalus pulicarius,* 38 *Deltocephalus configuratus* and 8 *Balclutha impictus.* But the large number of snails, sowbugs and millipedes found on it was the best index of how little of it the phytophagous insects ate, or the single mowing removed. The limiting factor for orchard grass in this meadow was lack of fertility, as it grew profusely wherever horses had been tethered to fences or trees and had supplied a sufficient amount of manure, but it did not occur elsewhere.

The insects specifically feeding on red clover found in the 13 square feet examined in which red clover was the dominant plant were: 1 nymph and 3 adults of the treehopper, *Stictocephala lutea,* of which the adult weighs .002 gr., and 10 nymphs of another treehopper, *Ceresa* sp.; 12 aphids on roots, and 21 aphids, *Macrosiphum pisi,* and 25 mealybugs, *Pseudococcus trifolii,* on aerial portions of the plant; 40 seed midges, *Dasyneura leguminicola;* and the following weevils; 19 *Tychius picirostris,* of which adults weigh .00047 gr., 20 *Phytonomus* spp., of which adults weigh .0015 gr., and 22 *Sitona hispidula,* of which adults weigh .001552 gr. Not one of these insects is comparable in size and in the amount of the vegetative portion of the plant eaten to *Hypera punctata* and the larva of *Feltia venerabilis* on white clover. The amount of injury to red clover caused by insects can not be so easily determined, however, as in the case of white clover, as its most serious pests attack the flowers and seeds. But despite the destruction of its seed by the midges and by *Tychius* and *Phytonomus* larvae, its spread was not

being prevented. In part, this was possibly due to late harvesting and the incidental and accidental re-seeding that resulted. The rootborer, *Hylastinus obscurus* Marsham, which is often the limiting factor elsewhere in preventing the perennial growth of clover when other conditions are favorable, was not found, although a careful search was made.

From the marked results obtained by the accidental application of manure in certain sections of the meadow, it is apparent that more even applications would have most beneficial results in favoring the growth of red clover and orchard grass throughout its area. Pasturing the aftermath, and possibly a second mowing late in the summer would also make a more economic use of the vegetation produced, and leave less to rot and feed the scavengers.

THE INSECTS FEEDING ON WEEDS

In the preceding computations, it has been taken for granted because of lack of any direct evidence to the contrary, that the omnivorous plantfeeders, such as crickets, grasshoppers, crane-fly larvae, white grubs and the grubs of Otiorhynchid weevils, feed on all the plants indiscriminately and directly in proportion to their abundance in the environments where the insects occur. If this is so, these general feeders constitute almost the only insects of considerable size and numbers to prey on the weeds, with very few exceptions. In the following list of insects found on specific weed hosts, Table 45, their small numbers and their insignificance in size is in striking contrast to the abundance of their hosts, which constitute 62.7% of the total vegetation in all environments. The insects number 545, a third as many as are found feeding specifically on grasses and clovers.

Of the meadow froghopper, *Philaenus spumarius* L., which appears to be the most common pest of weeds because it feeds on so many kinds of them, the adults weigh .0012 gr., and as the total number found was only 35, the injury caused to its numerous hosts was negligible.

The adults of the dandelion weevil, *Ceuthrohynchus marginatus* Payk., weigh .0008 gr. Thirty-two individuals were found in the meadow, where the dandelion constituted 3% of the vegetation, but as it took eight larvae to entirely destroy the seeds in one head, the injury caused by this insect was not sufficient to appreciably reduce the abundance of its host. The cows in the pasture of scant vegetation had reduced the amount of dandelion present to half of a percent, and to 1.5% in the other pasture. Obviously, they were a much more effective check on it than the weevils which were found only in the meadow.

The one really serious pest of a specific weed was the black Chrysomelid beetle, *Phaedon aeruginosus* Suffrian, which fed on Veronica.

TABLE 45. The Weeds and the Insects Feeding on them in the Grasslands at Barneveld, New York.

Weed	Percent of All Vegetation	Number of Insects	Insect
Narrow-leaved Plantain	12.3%	3	nymphs of froghopper, *Philaenus spumarius*
Sorrel	6.6	..	no insect
Buttecup	6.1	5	nymphs of Froghopper, *Philaenus spumarius*
		1	Lepidopterous Leaf-Tier Larva
		2	Chrysomelid beetles in flowers, *Prascocuris varipes*
		20	small Dipterous pupae in dead stem
Violet	5.6	1	Chrysalis of Butterfly, *Argynnis cybele*
		1	Lepidopterous Leaf-Tier Larva
Daisy	5.4	11	nymphs of Froghopper, *Philaenus spumarius*
		73	Thrips in flowers, *Haplothrips graminis*
		1	Beetle in flower, *Macrodactylus subspinosus*
		1	Crambid egg-cluster on leaf
Strawberry	4.8	7	grey Aphids on roots
		1	Lepidopterous Leaf-Tier Larva
		2	Beetles, *Otiorhynchus ovatus* (and
		2	constructive larvae)
Moss, *Polytrichum*	3.8	2	Byrrhid Beetles, *Cytlius sericeus*
		5	pink Mealybugs on roots
Veronica spp.	2.9	177	Chrysomelid Beetles and larvae, *Phaedon aeruginosus*
Oxalis	2.1	..	no insect
Dandelion	1.7	39	woolly white Aphids on roots, (with
		70	attendant Ants, *Lasius aphidicola*)
		4	Beetles, *Olibrus nitidus* and *O. apicalis*
		33	seed-destroying Weevils, *Ceuthorhynchus marginatus*
Blue Curl	1.5	..	no insect
Everlasting	1.2	8	Treenoppers, *Entylia carinata*
		17	Aphids, *Macrosiphum ambrosiae*, on stem
		1	chrysalis of Butterfly, *Pyrameis cardui*
Canada Thistle	1.	2	Treehoppers, *Campylenchis latipes*
Chickweed	.9	..	no insect
Yarrow	.7	1	Moth, *Platyptillia marginidactylia*
Lichens	.7	6	Aradid Flat-Bugs, *Acalypha lillianis*
Sedge	.6	..	no insect
Adder's Tongue	.5	..	no insect
Ironweed	.3	..	no insect
Fern	.3	..	no insect
Bluets	.2	7	Flea-Beetles on flowers, *Haltica rufa*
Aster	.2	..	no insect
Jill-over-the-Ground	.2	..	no insect
Broad-Leaved Plantain	.2	..	no insect
Dock	.1	10	Beetles, *Rhinoncus pyrrhopus*
Cornus sp.	.1	..	no insect
Cherry Trees	.1	1	Lepidopterous Leaf-Roller Larva
Devil's Paintbrush	.1	3	nymphs of Froghopper, *Philaenus spumarius*
St. Johnswort	.06	..	no insect
Plum Trees	.04	..	no insect
Moth Mullein	.02	..	no insect
Mint	.02	17	Mealybugs on roots
Foxtail Grass	.02	..	no insect
Maple Tree	.02	..	no insect
Apple Tree	.02	..	no insect
Basswood Tree	.02	..	no insect
		13	nymphs and adults of Froghopper, *Philaenus spumarius*, not on host

TABLE 46. A Comparison between the Amount of Veronica in the Grasslands at Barneveld, New York, and the Beetles Feeding upon It.

	Meadow	Scant Pasture	Abundant Pasture
Number of *Phaedon* per square foot:	.57	.61	7.17
Weight in Grams per square foot:	.0010715 gr.	.0011468 gr.	.0134796 gr.
Weight in Pounds per Acre:	.10288 lbs.	.1101 lbs.	1.29404 lbs.
Weight of Veronica in Pounds per Acre:	60 lbs.	108. lbs.	120. lbs.

No data were obtained on the digestibility of *Veronica* by *Phaedon*. If it were no more digestible than grass, then in the pasture of abundant vegetation the beetles ate 62.7 pounds of it, or half the amount present. If, as is more likely, it is nearly as digestible as clover, this would cut down the estimated amount eaten by the beetles to a quarter of the amount present in this pasture. In the other pasture and in the meadow, the amount eaten is negligible.

With the cows definitely avoiding half of the weeds and eating the others more by accident than by design, and with so few insects, aside from the general feeders, to eat them as compared with the large number of comparatively large insects specifically and exclusively feeding on the grasses and clover, it is not surprising that the weeds should constitute such a large part of the vegetation of the pastures. Indeed, it is an indication of their amazing power and recovery from the injury caused by the feeding of cows and insects that the grasses and white clover should continue to be such a large part of the vegetation of the pastures.

DISCUSSION

The results obtained in this investigation are somewhat tentative and preliminary to serve as a basis for outlining any specific measures for the improving of ordinary agricultural practises in the handling of pastures and meadows in general. They do, however, indicate the desirability of making similar studies elsewhere, on different soil types and in other regions.

No fundamental change in methods adopted for collecting the data is suggested as essential, for those used appear adequate for obtaining the desired results. They might well, however, be supplemented by sweeping with the insect net, principally to obtain a more complete record of the parasitic wasps, often too rare to be adequately sampled otherwise, but of such importance despite their rarity, that some more complete record, even if not quantitatively exact, should be obtained. The difficulties experienced in interpreting the results emphasize the importance of independently determining the rôle of *each* insect or other small invertebrate in its environment, for without an adequate conception of what each organism *does*, the problem of evaluating them in the mass is almost impossible. That is, of each animal it is essential to know not only its name, weight, and the varying numbers present

throughout the growing season, but also how fast it grows, what it feeds upon, the digestibility of its food and also what organisms feed upon it. Of not one of the common, dominant, economic insects and birds are these data available in detail, yet for properly interpreting a census, all this information concerning each species is essential. The problem seems almost hopeless for a single investigator to attempt within reasonable time, yet by intensive rearing the second season of the forms found of greatest importance during the first season, it may be solved, subject to considerable limits of error. No organism can be neglected because of its small size, yet in the present investigation, it eventually became obvious that a few large insects, the May beetles, cutworms, crickets and grasshoppers, bulked in importance in affecting their environment far greater than the numerous species of leafhoppers and ants which systematically occupy such a large place. A similar result may be anticipated in other similar investigations, and in apportioning the time and attention of the investigator, they might well receive more of it than was accorded them in this investigation. The same might be said of the small wild vertebrates, an accurate census of which from day to day throughout the season proves to be quite as essential as the detailed studies on the insects and vegetation. The investigator, indeed, must be a naturalist, interested in every organism, to properly evaluate the importance of each one, and to synthesize their combined impact on the area studied.

The economic importance to man of such investigations is greater because so few of them have been made. In the present instance, the farmer had long known that he was not obtaining the maximum benefit from the pasture containing the greater amount of vegetation, and eventually he solved this particular problem, to some extent, by fencing off part of this pasture and bringing it under cultivation. Actually, he didn't begin to solve his problem, which was that two-thirds of the pasture vegetation was weeds, which the cows could not, did not, or preferred not to eat, and that even when the carrying capacity of both pastures for stock was used to the fullest extent, the insects there ate approximately half as much of the grasses and clover as did the cows. This is less than 25% efficiency in the farming of such areas. If such a condition is at all general (and such can be determined only by a number of such investigations similar to this, on other types of soil and in other farming regions), it indicates the need of fundamental changes in the handling of pastures. Surely, in an age of machine farming, less than 25% efficiency in one important division can not long survive. Intelligent, progressive farmers would not think of tolerating such a condition in cultivated crops, but little change is to be anticipated in dairying until the facts are determined and the information becomes widely known.

SUMMARY

1. A total of 6,843 invertebrates was collected from one hundred square feet of grasslands on Merrimac fine sandy loam near Barneveld, New York, between April and October, 1919. Of the more important scavengers, there were 111 earthworms, 125 snails or slugs, nearly half of which were *Vallonia excentrica* Sterki, 123 sowbugs, *Porcellio rathkei* Brandt., and 623 millipedes, 612 of which were *Julus caeruleocinctus* Wood. Of the 470 spiders, half were very small Erigonids, and 94 *Pirata minutus*, but including quite a number of large species, and of the 174 mites, most were *Allothrombium* spp., or Gamasid nymphs, and often attached to a host insect.

2. The 93 springtails, *Tomocerus flavescens* Tullberg, which feed on decaying organic matter and fungi, were as insignificant in size as the 74 thrips, *Heliothrips graminis* Hood, that were found in daisy flowers. But the 69 grasshoppers, of nine species, and the 127 crickets, *Grillus assimilis* F. and *Nemobius vittatus* Harris, formed a fifth, by weight, of all the insects. Of the 121 Hemiptera, nearly half were *Geocoris uliginosus limbatus* Stal, a small insect of uncertain habits, but reputed to be predaceous. Over half of the 61 froghoppers were *Philaenus spumarius* L., notable because it was the only general pest of weeds noted. One thousand twenty-seven leafhoppers (447,371 per acre) were collected, of fourteen species. Of these, nearly half were *Acucephalus striatus* L., one-sixth *Acucephalus albifrons* L., and a tenth each *Xestocephalus pulicarius* Van D., and *Agallia 4-punctata* Provancher. But despite the numerical abundance of the leafhoppers, they formed, even where most abundant, only a twelfth by weight of all insects, and only a fortieth in the pasture with the scantiest vegetation. About half of the 124 aphids were aerial in habit; most of the subterranean ones were attended by a single species of ant, *Lasius aphidicola* Walsh.

3. The 66 noctuid larvae formed two-fifths of all Lepidoptera collected, and by bulk a much larger part. It is estimated that the most abundant species, *Feltia venerabilis* Walker, devoured nearly half of all the white clover eaten by all the insects specifically feeding on this plant.

4. The 22 threviid larvae and the 15 maggots of the crane-fly, *Pachyrhina ferruginea* F., occurring most often in the soil of the pastures, and the 42 larvae of the clover-seed midge, *Dasyneura leguminicola* Lintner, were possibly the most important of the 222 Diptera collected.

5. Of carabid beetles, 17 species, and of staphylinids, over 22 species were found, besides 83 elaterid larvae, or adults, mostly *Melanotus* sp., and 25 cantharids, mostly larvae of *Telephorus bilineatus* Say. Only one-twenty-fourth of the 623 beetles (excepting the Curculionidae) collected are definitely known to be harmful to the grass or clover, the others being beneficial or neutral, or, in the case of the wireworms, dependent on attending circumstances as to their status. However, the 25 members of the beetle genus

Lachnosterna, which numerically were such a small fraction, by weight constituted half of the beetle population. Of the beneficial beetles, 177 were of a small black chrysomelid, *Phaedon aeruginosus* Suffrian, which here fed on *Veronica*, a pretty little pasture weed.

6. Of the 515 Curculionidae, or weevils, most were species with subterranean larvae, and included many *Sitona hispidula* F. and *Sitona flavescens* Marsham, the adults of which feed on clover. There were 53 individuals of the larger clover-leaf beetle, *Hypera punctata* F., besides 23 *Phytonomus* spp., and 19 *Tychius picirostris* F., adults and larvae of both species feeding on clover. In one of the pastures, the white clover eaten by these curculionids and the clover cutworms amounted to a third as much as the cows ate, and if to this is added what other insects with less specialized feeding habits may have eaten, it totals half of what the cows ate. In the other pasture, where there were fewer cows, and more grasshoppers and crickets, it is estimated that the insects ate as much of the available clover as the cows did.

7. In point of numbers, the ants, 1,782 for the hundred square feet, exceeded any other form of animal life. The common ants were *Brachymyrmex depilis* Emery, *Myrmica emeryana* Forel and *Lasius americanus* Emery, and being either largely or entirely scavengers, their occurrence in such large numbers was possible only because of their small size. Of the other 40 Hymenoptera, 7 *Ophion bilineatus* Say, a parasite of the noctuid cutworms, and 1 *Tiphia transversa* Say, a parasite of white grubs, were the largest and possibly most important.

8. The insects specifically feeding on the distinctive meadow plants of economic value, the orchard grass and red clover, which did not grow in the pastures, were so scarce that it seems fair to assume that lack of soil fertility was apparently the limiting factor preventing their crowding out the weeds. The single mowing of the meadow removed only a small portion of the plant tissue produced, and here the plant scavengers, the millipedes, sowbugs, snails and slugs, flourished in greatest abundance.

9. The pastures examined seemed not exceptional or abnormal, but a fair average of those present for miles around, yet the grasses and clovers constituted only a third of the total vegetation, the other two-thirds being weeds, over half of which the cows would not eat. The insects specifically feeding on the weeds constituted only a third as many as those feeding on the grasses and clovers, and most of them were insignificant in size.

10. The robin, *Merula migratoria* L., was twice as abundant in these grasslands as all the other birds combined. A comparison of what it ate forty years ago in Illinois, as determined by Prof. S. A. Forbes, and what was available for the insect portion of its food in the meadow-pasture area in New York, shows in general outline, a most striking similarity. It indicates that the robin eats every insect of reasonable size that is present in the

closely grazed pastures that are its preferred hunting grounds. The exceptions were the Carabid and Histerid beetles, of which it ate vastly more, and the Elaterids, of which it ate many less, in proportion to the other insects present at Barneveld.

11. To determine how much of the economic grasses and clovers the larger and more abundant phytophagous insects noted in the pastures were eating, it became necessary to conduct feeding experiments. Expressing the data obtained in terms of the weight of the insects themselves made possible direct comparison with what the cows were obtaining from the pastures. Surprisingly enough, it was found that where there were few cows in the pasture, they scarcely equalled in weight the total of the wild life present there, and the insects ate more of the grasses and clovers than the cows did. Indeed, the cows obtained a larger share of the pasturage only where they kept the vegetation so short that it afforded scanty protection for the crickets, grasshoppers and leafhoppers, and was more attractive to the robins, who foraged there in greater numbers, and still further reduced the number of insects.

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FACTORS AFFECTING YEARLY ABUNDANCE OF PASSERINE BIRDS

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FACTORS AFFECTING YEARLY ABUNDANCE OF PASSERINE BIRDS[1]

INTRODUCTION

More exact and critical studies of the actual abundance of animals is of prime importance in furthering ecological knowledge. Such studies are of considerable theoretical interest in the pure science of ecology and also have a value for economics and conservation. The present study deals with a non-game species, the house wren, *Troglodytes aedon* Vieillot,[2] and attempts an analysis of the various factors, both biological and climatic, that cause variations in its abundance from year to year in the eastern portion of its range. Factors that cause variations in abundance may also be important in limiting distribution. The house wren is migratory in its seasonal behavior, the eastern form occurring in southern Canada and the eastern United States east of the Mississippi River and north of Kentucky and North Carolina in the summer, and in the south Atlantic and Gulf states in the winter. It is believed that this species is typical in its ecological reactions of, at least, the smaller migratory species of the order, Passeriformes.

In a previous publication (Kendeigh, 1934) the distribution and migration of this species were discussed in detail and the various controlling factors were considered. A preliminary graphical analysis was also made of the fluctuations in abundance of the species over a period of thirteen years.

In the present study, it was deemed important to carry this analysis of fluctuations in abundance considerably further, using statistical methods, in order to follow out certain leads that had been uncovered. In the previous report, the number of breeding birds was determined each year on an area of approximately fifteen acres (Area A) by trapping the adult birds at their nest-boxes and banding each individual with a differently numbered Biological Survey band. As this sampling area is small, an attempt is here made to correlate the fluctuations in population and amount of reproduction on this area with similar fluctuations on two other adjacent areas for those years in which comparable data are available (Table 1). All the areas are in the vicinity of Gates Mills, near Cleveland, Ohio.

In order to place population censuses upon a comparable basis they are figured as number of adult birds per nest-box available at the beginning of

[1] Contribution from the Baldwin Bird Research Laboratory (No. 31) and the Biological Laboratory, Western Reserve University, Cleveland, O.

[2] According to the *Checklist of North American Birds*, fourth edition, 1931, the subspecies here considered is *T. a. aedon*. According to a recent revision of Oberholser (Ohio Jour. Sci. 34 (2), 1934, 86-96), *T. a. aedon* is split into two subspecies and renamed *T. domesticus domesticus* and *T. d. baldwini*. The present study includes both of these subspecies, with chief concentration on the latter. The third and only other subspecies, *T. d. parkmanii*, is not here considered.

TABLE 1. Comparison of Yearly Fluctuations in population and reproduction of the House Wren on three different areas near Gates Mills, Ohio.

A - 15 acre sampling area; B - Gates Mills and vicinity; C - outlying estates.

Year	Available nest boxes			Variations from average for 9 year period. (Signs in parenthesis show direction of fluctuations from preceding year.)											
				Number of adults per box			Number of males per 100 females			Number of broods per female			Percentage during first breeding period of total broods for season		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
1926	31	91	..	—0.2	—0.2	.....	—39	—2	.....	—0.2	—0.2	.....	—27	— 4	.....
1927	31	94	..	—0.1(+)	+0.1(+)	.....	+23(+)	—22(—)	.....	0.0(+)	0.0(+)	.....	— 6(+)	— 5(—)	.....
1928	43	205	..	0.0(+)	—0.1(—)	.....	— 6(—)	+ 1(+)	.....	+0.1(+)	+0.1(+)	.....	—16(—)	— 8(—)	.....
1929	43	229	28	+0.1(+)	+0.2(+)	—0.3	+12(+)	— 8(—)	+ 4	+0.2(+)	0.0(—)	0.0	— 6(+)	0(+)	—15
1930	43	280	114	0.0(—)	0.0(—)	—0.5(—)	— 6(—)	— 8(=)	— 3(—)	0.0(—)	—0.1(—)	—0.2(—)	+15(+)	+ 4(+)	+ 4(+)
1931	43	245	59	—0.1(—)	—0.1(—)	—0.1(+)	— 6(=)	+ 4(+)	— 1(=)	—0.1(—)	0.0(+)	+0.1(+)	+ 2(—)	0(—)	— 4(—)
1932	47	241	56	—0.1(=)	+0.1(+)	+0.4(+)	— 6(=)	+ 1(—)	+ 2(+)	0.0(+)	+0.1(+)	0.0(—)	+ 8(+)	+ 5(+)	+ 2(+)
1933	47	166	65	+0.1(+)	+0.4(+)	+0.4(=)	—20(—)	+ 6(+)	— 5(—)	—0.2(—)	—0.1(—)	—0.1(—)	+26(+)	+ 3(—)	+14(+)
1934	47	166	58	—0.1(—)	0.0(—)	+0.2(—)	+44(+)	+29(+)	+ 2(+)	+0.4(+)	+0.2(+)	+0.1(+)	+ 1(—)	+ 1(—)	+ 1(—)
Average				0.5	1.0	1.3	106	102	96	1.4	1.3	1.4	56	61	57

the season (before June 1). On area A the number of boxes available were many more than could be possibly used, so that the average number of birds per box on this area is reduced considerably below the averages for the other two areas. It will be noted that, in general, fluctuations in abundance agree well on all three areas. The minor exceptions may be satisfactorily explained. The lack of agreement in 1928 may be accounted for by the more than doubling of the number of boxes available on area B during this year over the preceding year, to which increase the species did not have time to respond in normal proportion, particularly as some boxes were erected after the migration period was largely over. Perhaps the same explanation holds, in part, for the unusually low average of area C in 1930, although here the fluctuation in abundance from the preceding year agrees with that on the other two areas. The lack of agreement of area C in 1931, giving an apparent increase instead of a decrease, may be due to the elimination of a large number of the surplus boxes of the preceding year located in unfavorable situations. In 1932, there was actually an increase in number of birds over 1931 in area A (Table 2), as in areas B and C, but due to a slight increase in number of boxes, which is without particular significance in this area, the averages for the two years are the same. Likewise on area C in 1933 there was actually an increase over the preceding year in number of birds, amounting to 17 percent, but the increase in number of boxes keeps the average the same.

There is no correlation in the figures for sex ratio (number of males per 100 females) between areas A and B, although between areas A and C some correlation seems to exist provided a fluctuation is not indicated unless it amounts to more than two individuals. Two things may be considered in explaining the lack of agreement of area B with areas A and C. All the trapping of birds and census-taking on area A for all years was done by one person, probably with the same degree of efficiency. The same is true of area C, and this accounts for the agreement in yearly variations between this area and area A. On area B, at least seven different assistants have been employed during various years, and undoubtedly different efficiencies in census-taking were involved. In addition, on area A an attempt was made to capture all adult birds, but on areas B and C this was not always possible. On these latter areas, most of the females were captured but generally a smaller percentage of the males. On these latter areas, males that did not get mates and rear broods were mostly disregarded. This also explains the lower average sex ratio obtained on these areas than on area A.

The last two columns in the table, number of broods per female and percentage during first breeding period of total broods for the season, agree fairly consistently on the three areas. Thus it is seen that, in general, fluctuations in population and reproduction agree on all three areas. There is some reason to believe that the major fluctuations, at least, agree for even a larger portion of the breeding area of the species. This was certainly true

and verified by numerous reports in 1926, when there was a diminution in abundance of the species all over the eastern part of its breeding range. With this satisfactory check on the data, the further discussion in this paper will deal, principally, with the population on area A, immediately surrounding the research laboratory, since data on this area cover a longer period of years and were obtained with a greater degree of accuracy.

A recheck has been made of all the original records and notes on the number and breeding of the species on area A for each year, and another year's record has been added to those given in the earlier paper (Kendeigh, 1934, p. 307). A revised table here given (Table 2) corrects the data for certain years for number of birds and number of broods. This was made possible by a reinterpretation of some of the questionable records with the idea of eliminating even more strenuously than before any modifying influence caused by human interference. For example, when a female deserted a set of eggs, before she was captured and identified due to human or other interference, and a new set was laid at a nearby box within a few days, it was assumed that the female laying this new set was the same as had deserted the first. These two sets of eggs were likewise not counted in the totals as two broods but only as one. If a new nest was not started after the destruction or desertion of a first, the first was still included as one in the total of broods for that year, as the success or failure of nests is an entirely different problem, not of major consideration here. In the one or two instances when a bird was accidentally killed through handling or study, it was omitted from the totals for the year, but in the three or four instances when a female died from natural causes it was included. There is interest in this respect that in two such cases, the female was found dead in the nest with a well-formed egg part way down the oviduct. All sets of eggs completed before July 1 are counted as coming in the first breeding period of the year, all completed after July 1 are counted as coming in the second breeding period. This does not mean, however, that a female found for the first time with a brood after July 1 must necessarily have had a first brood somewhere else. Our records do not indicate that this is more than a rare occurrence as practically all nesting birds within a radius of approximately a mile from this area are identified by numbered bands and their nesting history known. Cases are negligible also of birds having a first brood in this area and then going elsewhere for a second. Table 2 does not include any possible non-breeding birds also present in this area, and most of the discussion in the paper is based on the data in this table. Further explanation of the table will be presented under appropriate headings later in the paper.

METHODS

Simple statistical methods were employed to determine the relative significance of the various factors effective in controlling yearly fluctuations in

numbers. In Table 3, the means of most of the items listed in Table 2 are given. In addition, computations were made to indicate the degree of variability of each item considered. Formulae for obtaining standard deviations and coefficients of variability may be found in Arkin and Colton (1934). It is sufficient to note here as to the significance of the standard deviation that if an indefinitely large number of samples were taken, 68 percent of them would fall within the limits set by the plus and minus standard deviation from the mean, provided other factors remained the same. The coefficient of variability merely expresses the size of the standard deviation in terms of percentage of the mean. These two criteria, along with the minimum and maximum, should give a good idea of the constancy or variability of each item in the table.

Extensive use was made in later tables of coefficients of correlation for determining the interrelation of two factors. Pearson's product-moment method was followed as it is outlined in Sinnott and Dunn (1925). The reader need not necessarily be acquainted with the details of this method for interpreting the tables if he keeps the following points in mind. A perfect positive correlation between two factors gives a coefficient of +1.0, a perfect negative, i.e. inverse, correlation a coefficient of —1.0, no correlation at all a coefficient of 0.0. It is seldom that a perfect positive or negative correlation is obtained, so the coefficients ordinarily given are decimal fractions. The size of the decimal fraction is a measure of the degree of correlation obtained.

Since the number of years covered in this analysis is rather few for treatment by the statistical method, the coefficients were adjusted according to formulae given by Arkin and Colton (1934) to compensate statistically for the small number of records involved and to avoid giving undue importance to the coefficients obtained. This reduced the size of all the unadjusted coefficients, frequently changing a slight plus or minus coefficient to zero. The standard error of each coefficient has about the same significance as the standard deviation explained above, i.e., if the true coefficient could be obtained from an indefinitely large number of samples there are 68 chances out of 100 that it would lie within the limits indicated by the standard error.

To determine the reliability of the coefficients of correlation they were divided by their standard errors. To eliminate the possibility that the correlation obtained is simply a matter of chance, the coefficients should be at least two, better three, times the standard error. Three times the standard error represents a percentage probability of 99.7 out of 100 that the correlation obtained is a true one, or, in other words, that there is only 0.3 percent likelihood (3 chances in 1000) of obtaining a correlation as high as that due to chance. A coefficient two times the standard error represents a percentage probability of occurrence of 95, one times the standard error a percentage probability of 68, while 0.67 times the standard error a percentage probabil-

ity of occurrence of only 50. These values were obtained from Pearl (1930, Appendix III, p. 439). In a few instances, recorded in the following tables, the percentage probability of occurrence turned out to be less than 50. Such low percentages indicate that the small correlations obtained are of slight or no significance. If the correlations obtained in all cases are significant ones, their percentages of probability will generally be raised when a larger number of yearly records are included. At the present time, the correlations obtained can be suggestive only, at least in a large number of cases.

The coefficients of correlation may also be low in some cases because several factors are simultaneously effective and their compensating or conflicting influences are not eliminated. It is possible statistically to eliminate the conflicting effects of these other factors through the use of coefficients of partial correlation (Pearl, 1930), and this was done in the first general correlations (Table 4).

Practically all the statistical computations were made on a calculating machine and all computations were rechecked at least once, so probably mere mechanical errors have all been eliminated.

In the tables that follow the various factors are listed according to the size of the coefficients of correlation and their probability of occurrence. This is in order to give greater emphasis to those correlations that seem to be best established statistically. Those correlations of less statistical significance should not, however, be automatically discarded since they are suggestive and may prove of greater significance with the accumulation of a larger number of records.

LITERATURE

There has been very little organized study of the factors affecting the yearly fluctuations in abundance of passerine birds. More information is available on game (mostly non-passerine) species than on non-game species. In an earlier publication (Kendeigh, 1934), a review was made of much of the literature and also a discussion of the physiological bases for many of the correlations to be brought out in this paper. There is no need to repeat that information here except to quote the conclusion arrived at as a result of the graphical analysis of the factors affecting fluctuations in the abundance of the house wren: "Variations in the abundance of a species in the same locality during consecutive years is dependent upon the number of birds breeding during the previous year, the amount of reproduction, and the survival over winter. The reproductive activities of individual birds varies from year to year inversely to fluctuations in numbers of breeding pairs of that species in the area. The relative amount of reproduction is correlated positively with average night temperature and inversely with velocity of wind and number of enemies. Variations in rate of survival over winter are correlated positively with variations in average night temperature, relative humidity, solar radia-

tion, and precipitation and inversely with velocity of wind. These factors vary in their relative importance during autumn, winter, and spring."

YEARLY FLUCTUATIONS IN NUMBERS

The yearly variability in the house wren population is close to 20 percent (Table 3). This is not as great as in some other species of birds nor in some mammals, but is sufficiently large to invite investigation as to its causes. Larger yearly fluctuations occur particularly in those species subject to epidemic disease. There is no present evidence for the occurrence of such epidemics in this species, although no special study of diseases has been undertaken.

An examination of the data on total number of adult birds each year (Table 2) shows three peaks in abundance (1922, 1929, 1933) and two depressions (1926, 1931). The intervals between these points are 7, 4, and 5 years respectively. It may be possible that this species shows cyclic trends in its abundance (Wing, 1935), but the present data are too inadequate to affirm or deny this point. If such a cyclic type of fluctuation does exist it may be secondary, dependent upon the cyclic fluctuation in some one or more important affecting factors—not upon the cyclic incidence of epidemic disease.

Yearly fluctuations in the numbers of the two sexes do not always agree perfectly. The coefficient of correlation between yearly numbers of males and females is $+.409 \pm .240$. The coefficient is 1.7 times the standard error, thus indicating a probability of occurrence for such a correlation of 91 percent. This is fairly high, meaning that the number of individuals in the two sexes are generally correlated in their fluctuations. The coefficient of variability of the male (Table 3) is slightly greater than of the female. Reference to Table 2 shows that in the two years of depression, the males were fewer in number than the females in one year and the same in the other. In the three years of maximum abundance, the males were more abundant than the females during two years. The maximum and minimum yearly numbers of males are further apart than they are for the females. The coefficient of correlation between the total number of adult birds present yearly and the yearly sex ratio (number of males per 100 females) is $+.356 \pm .252$. The coefficient is here 1.5 times the standard error, indicating an 87 percent probability of occurrence. The coefficient of correlation between the number of females taken separately and the yearly sex ratio is zero. If the unusual year, 1926, is excluded the correlation is negative ($-.449 \pm .241$; 1.9 times the standard error; 94 percent probability) indicating that when the most unfavorable years are excluded, the sex ratio is naturally smaller the larger the number of females present. The correlation between the number of males and the sex ratio is very high as one would expect ($+.749 \pm .127$; 5.9 times the standard error; 100(-) percent probability). These data indicate that

the male in this species is somewhat more sensitive to influencing factors, probably climatic, than is the female. Possibly this in turn may be correlated with the less weight of the male (10.8 grams) than of the female (11.4 grams) and consequently the lower resistance to unfavorably low temperature (Kendeigh, 1934). In order to explain the more rapid increase of the male than the female during favorable years, one supposition may be that in the sex ratio of nestling house wrens the males predominate. The sex ratio of nestling house wrens is not known, although the mean sex ratio of adult birds during the breeding season is close to 110 males: 100 females.

FACTORS AFFECTING YEARLY ABUNDANCE

It seems almost axiomatic that at least the three following major factors would be involved in determining the abundance of a species from year to year. The first factor would be the number of adults at the beginning of the breeding season. This would give the general rank of abundance, providing the other two factors were normal, and determine whether the species would be considered abundant, common, or rare. Likewise variations in the number of these birds might well affect the number of birds the following year. The second factor involved is the amount of reproduction, measured here by the percentage increase in total number of individuals due to the raising of young during the breeding season. The third factor is the loss in number or mortality of adults and young during the year, calculated as the decrease in total number of adults and young from the breeding season of one year to the

TABLE 2. Data on yearly populations, reproduction, and losses of the house wren on fifteen acres (Area A).

Year	Number adults			Sex ratio: number of males per 100 females	Number broods			Percentage during first breeding period of total number of broods	Broods per female	Number of young raised	Percentage increase in total number	Polygamy		Median date of starting first broods	Date of arrival of first individual	Yearly loss	
	Male	Female	Total		First breeding period	Second breeding period	Total					Number of cases	Percentage of total broods			Decrease in Number	Percentage decrease
1921	11	9	20	122	8	8	16	50	1.8	64	320	0	0	May 25	April 23	59	70
1922	16	9	25	178	9	6	15	60	1.7	61	244	0	0	May 23	April 10	65	76
1923	10	11	21	91	8	6	14	57	1.3	57	271	1	7	May 31	April 23	59	76
1924	10	9	19	111	7	6	13	54	1.4	53	279	0	0	May 29	April 13	55	76
1925	8	9	17	89	7	7	14	50	1.6	56	329	2	14	May 22	April 4	63	86
1926	4	6	10	67	2	5	7	29	1.2	27	270	1	14	June 5	April 18	21	57
1927	9	7	16	129	5	5	10	50	1.4	40	250	1(1[1])	10(0[2])	May 25	April 21	36	64
1928	10	10	20	100	6	9	15	40	1.5	59	295	1	7	May 23	April 22	55	70
1929	13	11	24	118	9	9	18	50	1.6	72	300	0	0	May 26	April 7	76	79
1930	10	10	20	100	10	4	14	71	1.4	59	295	1	7	May 18	April 26	61	77
1931	9	9	18	100	7	5	12	58	1.3	49	272	1	8	May 24	May 1	47	70
1932	10	10	20	100	9	5	14	64	1.4	57	285	0	0	May 24	April 21	51	66
1933	12	14	26	86	14	3	17	82	1.2	73	281	2	12	May 25	April 14	79	80
1934	12	8	20	150	8	6	14	57	1.8	57	285	0(2[1])	0(−14[2])	May 24	April 7	..	..

[1]Cases similating polyandry. [2]Percentage when cases similating polyandry are counted as minus values.

TABLE 3. Averages and variability of yearly populations, reproduction, and losses of the house wren on a fifteen acre sampling area (Area A).

Item	Mean	Minimum	Maximum	Standard deviation	Coefficient of variability
Number of males	10.3	4	16	± 2.6	25.2
Number of females	9.4	6	14	± 2.1	22.3
Total adults	19.7	10	26	± 3.9	19.8
Sex ratio: number of males per 100 females	109.6	67	178	±27.3	24.9
Number of broods during first breeding period	7.8	2	14	± 2.6	33.3
Number of broods during second breeding period	6.0	3	9	± 1.7	28.3
Total broods	13.8	7	18	± 2.7	19.6
Percentage during first breeding period of total number of broods	56.5	29	82	±11.7	20.7
Broods per female	1.5	1.2	1.8	± 0.3	20.0
Number of young raised	56.0	27	73	±11.4	20.4
Percentage increase in total number	284	244	329	±22.6	8.0
Percentage polygamous cases of total number of broods	5.2	0	14.0	± 4.3	82.7
Median date of starting to nest	May 25	May 18	June 5	± 4.2	....
Median date of arrival of first individual	April 21	April 4	May 1	± 8.3	....
Percentage yearly losses	72.8	57	86	± 7.3	10.0

beginning of the breeding season the next year. Presumably, fluctuations in any one of these three factors, unless compensated for by variations in one or both of the other factors, would affect the abundance of the bird from year to year. It would seem also that any biological or climatic factor that influences abundance must do so through an affect on one of these three factors. If the foregoing argument is true, a high coefficient of correlation would be expected between yearly number of birds and each of these three factors, particularly if the method of partial correlation is used. Table 4 gives the actual values obtained.

TABLE 4. Factors affecting yearly abundance (Based on use of coefficients of partial correlation).

Factor	Coefficient of correlation	Standard error	Coefficient divided by error	Percentage probability of occurrence
Losses during year	—.505	± .225	2.2	97
Number of adults preceding year	+.478	± .233	2.1	96
Percentage increase during preceding breeding season	+.206	± .289	0.7	52

The coefficients of correlation are not as high as was expected. This may be due in part to the omission of the non-breeding birds in the yearly population figures. Likewise, it may be that the sampling area was too small to adequately represent minor variations in the whole species population of the house wren. Variations in these three factors on the sampling area may be partly offset by reverse variations of the same factors in other regions with the subsequent moving into or out of the sampling area of birds not accounted for in this manner of statistical treatment. There are always many records each year of new unbanded, presumably young, birds invading the sampling area and apparently the dispersal of birds from the sampling area

into surrounding regions does not always compensate for this. There thus seems to be a yearly shifting of surplus population, probably young birds, from one locality to another that compensate for unevenness in the abundance of the species as determined by local variations in conditions. Therefore, in considering the fluctuations in abundance of a species in local regions this fourth factor must be taken into account, although it may be eliminated where it is possible to obtain an adequate sample of the whole population of a species.

In spite of the small size of the sampling area, the uncertain number of non-breeding birds each year, and the compensating influence of shifting populations, the coefficients of correlation are sufficient to emphasize the importance of each factor. The low value of the correlation with percentage increase (reproduction) may indicate either that this factor is of less importance or that fluctuations in the amount of reproduction on this sampling area is less adequate as a criterion for the regional population of the species than are fluctuations of the other two factors.

In the further analysis of this problem, special attention will be paid to the factors affecting the amount of reproduction and the yearly losses. The number of adults the preceding year is determined by the interaction of amount of reproduction, yearly losses, and shifts in population during the year before. Data for the analysis of local shiftings in surplus population are gradually being accumulated through banding operations, but an analysis of this problem must await special studies.

FACTORS AFFECTING AMOUNT OF REPRODUCTION

In considering the amount of reproduction it is necessary to analyze several different aspects. Since the amount of reproduction has been considered as percentage increase during the breeding season, this will be considered first.

Percentage increase—In computing percentage increase in number of birds during each breeding season several items were involved. The number of broods during the first and second breeding periods had to be figured separately. In a summary of data for years 1921 to 1930, it was found that the average number of eggs for each of 67 first sets was 6.5 and for each of 50 second sets was 5.2. To determine the total number of eggs for each year the numbers of first and second broods were multiplied by the respective average number of eggs per set. Of 133 house wren nests whose outcome is known, 68.4 percent were successful in having at least one young leave the nest. The total number of eggs for each year was then multiplied by this percentage to give the number of young birds raised. The number of young raised divided by the number of adults at the beginning of the season gives the percentage increase used in this study. The number of young raised is obviously approximate only because the percentage of eggs laid from which

young are raised is smaller than the percentage of successful nests. However, this discrepancy is of less importance than the fact that it was impracticable to utilize for each year separately the exact number of eggs laid and the percentage of young raised. These latter figures would be difficult to determine on this particular area (A) because of the frequent use of the eggs and young for other experimental purposes. Variation in these factors constitutes a special problem in itself requiring special analysis which may be undertaken in the future.

The only obvious and statistically significant correlation obtained was between percentage increase in number and the total number of broods during the season ($+.307 \pm .261$; 1.2 times the standard error; 77 percent probability). Such a correlation was to be expected although not necessarily a high one since the increase is here measured in percentage, not in terms of absolute number of young raised. No correlation was obtained with percentage of the total number of broods coming during the first breeding period, although with a larger percentage of first broods one would have expected, because of the slightly larger number of eggs in these sets, a greater proportionate increase in numbers. Percentage increase in number was found not to be correlated with number of adult birds present.

Total number of broods—The factors to be correlated with total number of broods per breeding season are given in Table 5.

TABLE 5. Factors affecting total number of broods per breeding season.

Factor	Coefficient of correlation	Standard error	Coefficient divided by error	Percentage probability of occurrence
Number of females	+.766	±.119	6.4	100 (–)
Percentage during first breeding period of total number of broods for the year	+.455	±.229	2.0	95
Broods per female	+.357	±.252	1.4	84

The correlation between total number of broods and total number of females is logically correlated in a very high degree. The correlation was made with number of females rather than with total number of adults because the females are of greater importance in this connection, and, as will be seen later, there are variations in the breeding behavior of the birds to compensate for an unusually high or low ratio of males. The number of broods per female is a factor also of obvious importance in affecting the total broods for the season.

The correlation with the percentage during first breeding period of the total number of broods for the year was unexpected. There are two breeding seasons for this species each year, the first beginning in late May, the second in early July. This correlation indicates that the larger the number of broods started in May the larger the total will be for the year. At first, one might expect that the total number of broods would not be affected by

whether the broods came during the first or second breeding periods. However, the species may be adjusted to nest normally in May and June at the time of the first breeding period because of length of day and other factors, and if certain conditions, such as weather, are not then favorable some individuals will not nest at all during the year, even if these weather conditions later become suitable in July. That this explanation is probably correct is indicated further in Table 6 where a very high correlation was found between percentage broods during first breeding period and total number of females breeding during the year.

The size, constitution, and importance of the non-breeding population are of considerable interest and the following attempt at analysis is made. During the breeding seasons of 1920 to 1934, inclusive, 624 return records on adults handled the preceding year on all three areas, A, B, and C, were obtained. Of this number, 525, or 84.1 percent, were captured during the first breeding period of the season in May and June, while 99, or 15.9 percent, not until the second breeding period in July. This species is caught only in its nest-boxes, so if any birds do not nest their presence cannot readily be noted. A slightly greater percentage of females (87.5) was caught during this first period than of males (81.0). It is difficult to say what proportion of those not caught until the second period may have attempted unsuccessfully to nest or were missed otherwise in the trapping and banding operations. If these were known, the proportion omitting the first period would be smaller than here represented by the 15.9 percent. This figure represents an estimation of the maximum number of non-breeding birds during the first breeding period in this return adult population. An estimation of the minimum size of the non-breeding population at this time may be taken as zero, although this is very probably too low.

Considering now the birds that were banded during the preceding year not as adults but as nestlings, of which there are 151 in number, 108, or 71.5 percent, were trapped during the first breeding period and 43, or 28.5 percent, not until the second period. The distribution of males and females between the two breeding priods was almost identical. This is a considerably greater lag in initiating breeding than among the adult birds. If the 15.9 percent of adults not recorded during the first period entirely represents an unavoidable failure in the trapping operations (which is improbable), the same degree of failure would hold for nestlings, yet there would still remain 12.6 percent of the return nestling population that did not breed during the first period. The true number of non-breeding young birds probably lies between these estimations of minimum and maximum percentages (12.6 percent, 28.5 percent).

Another line of evidence is available involving additional non-breeding birds, i.e., in the records of birds omitting an entire year or more in their breeding record. Omission of breeding during certain years could only be

determined if the birds were recaptured during a subsequent season. Adult birds as a rule (see evidence beyond) return to nest repeatedly in the same region, so if they are not recorded during any year, they either did not nest or this omission must be due to failure in the trapping operations. There are records over this period of years of 38 omissions by adults of nesting for entire seasons, and this does not include other birds that may have omitted one or more years but were not recaptured. This number represents 5.7 percent, a maximum estimation, of the total adults that were probably present in the locality, about equally divided between males (5.5 percent) and females (6.0 percent).

An unexpectedly large number of immature birds, banded as nestlings, were found to omit one, less commonly two, years before they were recorded breeding. The number of such records is 33, or 17.9 percent, the maximum estimation, of the total return immature population. It is not likely that these birds nested elsewhere during these omitted years (see evidence beyond). The percentage of males that omitted the first one or two years (23.4) was found unexpectedly to be considerably higher than the percentage of females (6.7). This may or may not be accidental. If the omission of years in the breeding record of adult birds represents failure in trapping the birds, there still remains a percentage of 12.2 immature birds unaccounted for, the minimum estimation.

Allowing for this percentage of the total population that does not breed at all during the year, the percentages of breeding and non-breeding birds among the total return adults and return nestlings will fall within the following ranges, the extremes representing maximum and minimum estimations:

Breeding adults during first breeding period	79.3%	to	100 %
Non-breeding adults during first breeding period	20.7%	to	0 %
Breeding young birds during first breeding period	58.7%	to	76.7%
Non-breeding young birds during first breeding period	41.3%	to	23.3%
Breeding adults during second breeding period	61.0%	to	77.0%
Non-breeding adults during second breeding period	39.0%	to	23.0%
Breeding young birds during second breeding period	45.2%	to	59.1%
Non-breeding young birds during second breeding period	54.8%	to	40.9%

The percentages given in the above and following tables for the second breeding period were calculating theoretically on the basis that the number of second broods is to first broods as 43.5: 56.5 (Table 3), and that this ratio holds equally true for older and younger birds.

In order to get the percentage of breeding and non-breeding birds in the total population of the area it is first necessary to know the proportion of young birds (first breeders) to adult birds. This proportion may be approximately obtained if all unbanded birds captured in the area are considered first breeders, for which assumption supporting evidence is considered beyond. Between the years 1920 and 1934 (omitting years 1926 to 1930 with

expansion of trapping operations into new areas), of 1534 records of nesting wrens, 72.6 percent were probably first breeders (new unbanded birds plus return nestlings) and 27.4 percent were known to be return adults. Using these percentages and combining figures for adult and young birds, the percentages of breeding and non-breeding birds in the total population are as follows:

Breeding during first breeding period.....63.8% to 82.5%
Not breeding during first breeding period.....36.2% to 17.5%
Breeding during second breeding period.....49.1% to 63.5%
Not breeding during second breeding period.....50.9% to 36.5%
Breeding at some time during either first or second breeding period.....85.1% to 90.8%
Not breeding at some time during either first or second breeding period..14.9% to 9.2%

Considering the non-breeding population by itself, the proportion of adults and young birds will lie between the following maximum and minimum figures:

During first breeding period:
  Adult birds .....14.1% to 0%
  Young birds .....85.9% to 100%
During second breeding period:
  Adult birds .....19.0% to 15.7%
  Young birds .....81.0% to 84.3%
Not breeding during either period:
  Adult birds ..... 9.3% to 0%
  Young birds .....90.7% to 100%

It is difficult to make any definite statement as to the proportions of the sexes in the non-breeding population. Except for the data indicating that a greater proportion of young males than young females omit one or more years before breeding for the first time, the proportion of sexes would be about equal. If this exception is substantiated by later data, a preponderance of males would seem to occur.

Percentage during first breeding period of total number of broods for the year—There is a positive correlation between percentage of total broods during the first period and number of females present (Table 6). This correlation may have a greater indirect than a direct significance. A large

TABLE 6. Factors affecting the percentage of total number of broods for the year coming during the first breeding period.

Factor	Coefficient of correlation	Standard error	Coefficient divided by error	Percentage probability of occurrence
Number of females	+.678	±.156	4.3	100 (-)
Average night temperature during May, June, July	+.603	±.184	3.3	100 (-)
Time of beginning to nest	—.464	±.227	2.0	95
Precipitation during May, June, July	—.448	±.231	1.9	94
Wind velocity during May, June, July	+.293	±.264	1.1	73
Relative humidity during May, June, July	—.226	±.274	0.8	58

number of females generally indicates a favorable past winter for survival and, as suggested above, also a favorable early breeding season.

Climatic factors seem important here. Climatic data were obtained from the Cleveland Weather Bureau Station. From this table there is a good positive correlation with average night temperature which has previously been shown (Kendeigh, 1934) to be the most significant factor in the resistance of birds to low air temperature. This correlation is still higher if the night temperature for May and June only are considered. A careful study of the records for the various years indicates that the percentage of broods coming during the first breeding period drops below average when the average night temperature for May, June, and July falls below 62° F. (17° C.) or when the average night temperature during May and June falls below 58° F. (14° C.). There is also a good negative correlation with precipitation during the breeding season and a slight negative correlation with relative humidity. The fair positive correlation with wind velocity is of questionable significance since it is not supported by physiological experimentation—a negative correlation would have been expected. No correlation was obtained with percentage of total possible daily sunshine during May, June, and July, nor with the sex ratio.

In analyzing still further the effect of climatic factors, especially temperature, a statistical correlation attempted between the yearly percentage is of broods during the second breeding period and variations in the generally higher average night temperature during July proved to be zero. An attempted correlation between percentage of broods during the second breeding period and the higher mean daily maximum temperature during July also proved to be zero. In both cases a small negative correlation actually occurred before the correlation was adjusted for the small number of records. In fact, the coefficient of correlation with daily maximum temperatures during July was 1.0 times the standard error. It appeared that mean daily maximum temperatures above 80° F. (26.7° C.) were unfavorable. There may be some significance in that the high positive correlation between percentage broods during the first period and temperature did not express itself also as a positive correlation between percentage broods during the second period and temperature. One is tempted to interpret this zero correlation with temperature during July as signifying that high daily maximum temperatures are unfavorable for reproduction in this species, in fact, sufficiently unfavorable to eliminate the beneficial effect of the higher night temperatures at this time. Such an interpretation seems especially significant in connection with the correlation made in the previous publication (Kendeigh, 1934) between the southern limits of distribution of the species and the apparently controlling influence of higher mean daily maximum temperatures.

The good negative correlation with time of beginning to nest is probably an indirect one, as time of beginning to nest is determined largely by climatic

conditions (see beyond). If time of beginning to nest were directly correlated with percentage broods during the first period a positive correlation would have been expected, i.e., the earlier the birds started to nest the more time would be available for raising second broods and the lower would be the percentage of first broods in the total. In contrast to this the earlier the birds start to nest the larger is the percentage of broods during the first breeding period.

Percentage of total broods during the first breeding period is not correlated with number of broods per female. The reason for this is that during favorable years, as in 1933, the percentage of first broods is unusually high (82 percent) while during distinctly unfavorable years, as in 1926, there is an almost correspondingly greater percentage of second broods (71 percent), although the number of broods per female averaged the same (1.2) during both years.

If the above arguments are true, the following picture of the controlling influence of climatic factors, particularly temperature, upon the percentages of broods during the first and second periods is possible. When night temperatures during the breeding season are high, conditions become favorable for breeding earlier. Not only does nesting start sooner but a larger number of females undertake a brood, including some females which would not otherwise nest until later or not at all. However, with generally higher temperatures during this period, when the time comes for second broods in July, the daily maximum temperatures are now so high as to be discouraging, so that fewer second broods are started. On the other hand, during years with unfavorably low night temperatures early in the season, fewer birds attempt to nest and those that do nest delay it as long as possible until more favorable climatic conditions come later in the season. Then when the normal time comes for second broods, night temperatures have now become higher and more favorable and more birds begin to nest, although apparently not all nor as many as would have nested during the season had the first period been favorable. With the temperature during the season generally lower, the daily maximum temperatures do not become extreme nor exert an inhibiting influence. Likewise those birds that did attempt first broods may be encouraged by the more favorable climatic conditions to attempt second broods, provided they were not so long delayed in starting their first broods but that they are still in full reproductive vigor. Other climatic factors, as precipitation and to a lesser extent relative humidity, play contributing rôles. The importance of changes in length of day is not fully apparent. It may be that fewer birds undertake breeding in July, even when the temperature and other factors are favorable, because the length of day is diminishing and retrogression has already begun in the functional condition of the gonads.

Broods per female—The number of broods attempted per female is significant in showing the reproductive vigor of the birds and the influence of various factors (Table 7).

TABLE 7. Factors affecting number of broods per female.

Factor	Coefficient of correlation	Standard error	Coefficient divided by error	Percentage probability of occurrence
Sex ratio	+.697	± .148	4.7	100 (-)
Number of females: all years	0	.....	....	..
Number of females: excluding 1926	—.419	± .238	1.8	93
Percentage of total possible daily sunshine	+.324	± .258	1.3	81
Time of beginning to nest	—.317	± .259	1.2	77
Average night temperature during May, June, July	+.149	± .282	0.5	*
Wind velocity during May, June, July	—.122	± .284	0.4	*

*Less than 50, probably insignificant.

Sex ratio, a biological factor, appears to be most important in affecting broods per female. Apparently the greater extent that the number of males exceeds the number of females, the greater the opportunity afforded the females of finding proper mates for raising two broods.

The correlation with number of females is indirect. If all years are included no statistical correlation exists; if the abnormal year of 1926 is excluded, an inverse correlation appears. As seen earlier in this discussion, the number of females and the sex ratio are correlated inversely if the year, 1926, is omitted, but show no correlation if it is included. It appears, therefore, that the correlation between number of broods per female and the number of females present is a reflection of the sex ratio factor.

The correlation with time of beginning to nest is an independent one, indicating that the earlier a female starts its first brood the more time and opportunity will be left for finding a mate and rearing a second brood. The correlation is not high because of the important modifying influence of climatic conditions already discussed. As indicated above, the number of broods per female is not correlated with percentage of broods in the first breeding period.

The correlations with the climatic factors indicate that climate, as a direct factor, is of less obvious importance in affecting broods per female than the biological factors. The reason for this has already been given. Actually, the influence of climate is considerable. The number of broods raised per female is high during years with moderate weather conditions and when nesting can start early in May and is reduced when weather conditions, especially temperature, are extreme in either direction. The coefficient of correlation is low because of the cancelling effect of these extreme years. It is of interest that the climatic factor of greatest apparent significance in this table is not temperature but percentage of total possible daily sunshine. No correlation was obtained with relative humidity or precipitation.

Thirty-eight records are available on 16 banded females for determining the effect of age on number of broods raised per year. There are 15 records for birds one year old, 13 for birds two years old, 7 for birds three years old,

2 for birds four years old, and 1 for a bird five years old. No correlation with age was obtained. Apparently age does not affect the number of broods raised up to, at least, four or five years. In nature, it seems probable that birds do not live long enough for any possible effect of senility on reproduction to become expressed.

Sex ratio and polygamy—It is, of course, advantageous to the species, if its numbers are to be maintained or increased, to raise the largest number of broods possible. The species would be benefited if each female were able to raise two broods each year instead of one. Since in this species, the female remates for a second brood in the same season regardless of whether the male is the same one she had for the first brood or is a different one, a high sex ratio is advantageous. This allows the female plenty of opportunity for finding another mate and possibly for selecting between two or more males. A high sex ratio in the species is indicated, except that during unfavorable years, when it would seem most needed, it is greatly reduced, for reasons stated earlier in this paper. Compensations in breeding behavior occur to offset in part the wide fluctuations in sex ratio. These compensations consist in trends toward polygamy during some years and toward polyandry in others.

The coefficient of correlation between sex ratio and the polygamous tendency is $-.763 \pm .121$. The coefficient is 6.3 times the standard error which gives a percentage probability for the occurrence of such a coefficient of nearly 100. In obtaining this coefficient, all cases tending towards polygamy were considered as plus, and all cases tending towards polyandry as minus, and these were then expressed in percentage of the total number of broods (Table 2). Thus during unfavorable years when the sex ratio is greatly reduced, there is a strong tendency toward polygamy, i.e., of one male having two mates simultaneously, thereby increasing the recuperative powers of the species. On the other hand, during favorable years, when the sex ratio is high, polygamy is rare. During such years, there are not enough females to allow each male a mate, and so the total reproduction of the species is not so high as it would be if all the males were able to take part. During such years there is a tendency toward polyandry, which is not so highly developed, however, as is the tendency toward polygamy during poor years. It is not so vital to the welfare of the species.

Polyandry is usually defined as meaning a female having two mates simultaneously. In the strictest sense, it means a female copulating with two or more males during the same egg-laying period. In the present study, this definition is modified to mean a female caring for two nests or broods of young simultaneously. This is not true polyandry as the female may well have lost interest in the male of one nest while she was active at her other nest, but for want of a better term the cases detailed below will be considered

as *tending toward* this polyandrous condition. A similar broad interpretation of polygamy is also used in this study, although a few instances of polygamy in the strict sense are known to have occurred. In the following cases tending toward polyandry, it should be borne in mind that ordinarily the female cares for the young from her first nest for nearly two weeks before starting her second nest.

CASE 1, 1927, female No. 94248

First nest, mate: No. 94242	Second nest, mate: No. 94222
July 24—Young 14 days old female caught at nest and banded.	No activity here, no nest in box.
July 25—Only female feeding young in nest.	Female visits box with male about 5:00 P.M.
July 26—Young birds still in nest.	Male active carrying in sticks and female carrying in some nest lining.
July 27—Young birds left nest today.	Female carrying in more nest lining.
July 30—No observations.	First egg laid.
July 31—Female caring for young out of nest, male heard singing near old nest.	Second egg laid.
Aug. 1—No further observations on female here.	Third egg laid.
Aug. 30—No activity at nest.	Female captured, nestling birds in nest.

The female did not desert the first nest for the second nest but apparently alternated activities between caring for young from the first nest with building and laying eggs in the second. The sex ratio during this year was 129 males: 100 females. The very late date for completing the first nest may also have been an unconscious factor concerned in some way in inducing the female to get the second nest started as early as possible.

CASE 2, 1934, female No. L-24101

First nest, mate: No. H-18600	Second nest, mate: No. L-24996
June 10—Young 4 days old, female captured at nest.	Male here occasionally.
June 19—Young 13 days old.	Male singing here.
June 20—Young escaped, replaced.	Both male and female here, female active at nest building.
June 21—Young in nest, not being fed frequently.	Male active here, female not seen.
June 22—Young left nest in early morning.	Female carrying in nest lining in morning.
June 23—Both adults caring for young out of nest.	Female very active at building nest-lining.
June 24—No observations on adults.	More lining.
June 25—Male active at old nest.	More lining.
June 26—No further activity.	First egg laid.
July 17—No activity here.	Female captured, nestling birds in nest.

CASE 3, 1934, female No. L-24955

First nest, mate: No. F-45987	Second nest, mate: No. F-45987
June 15—Female captured, young 5-6 days old.	Mate active here, good male nest.
June 22—Young 12-13 days old.	Female carrying in first nest lining.
June 23—Young O.K.	More lining.
June 24—Young O.K.	More lining.
June 25—One young leaves nest.	More lining.
June 26—Last young leaves nest.	First egg laid.
June 27—Nest the same.	Second egg laid.
June 28—Male cleaning nest.	Third egg laid.
June 29—Male cleaning nest.	Fourth egg laid.
June 30—Male cleaning nest.	Fifth egg laid.
July 19—No activity here.	Female captured, nestling birds in nest.

In Case 2, it is clear that the female did not desert the young in the first nest to start the second as she was found with young out of the nest on June 23. There is no evidence in Case 3 that the female did not desert the first nest but if she did she remated with the same male at the second nest. Since the young in the first nest left in good order they must have been cared for by at least one and probably both adults. It is possible that when the female first started her second nest she was mated with a different unknown male and that later this unknown male was replaced by the old male from the first nest, since the male was not caught for identification until after the eggs had hatched, but there is no direct evidence of this. The sex ratio for this year was 150 males: 100 females.

Time of beginning to nest—The time of beginning to nest affects the percentage of total broods coming during the first breeding period and number of broods per female. The time of beginning to nest is the median date for laying of the first egg in all of the first sets during that particular year. This median date was obtained by ranking in chronological order the dates of laying the first egg in the first set of each female and then alternately crossing out the earliest and latest data until the median was reached.

The first correlation attempted was with the date of arrival of this species in the spring migration. The only usable information here was the date of arrival of the earliest individual in the whole region and no correlation with time of beginning to nest was found. It is possible that a correlation with time of arrival might be found if information were available as to the median date of arrival of the particular birds nesting in the particular area under observation.

Correlations between time of nesting and various climatic factors were next sought. Average data on each climatic factor for Cleveland and for the month of May were used. No statistical correlation was found with relative humidity, precipitation, velocity of wind, or percentage of total possible daily sunshine. A fairly good negative correlation was found with the average night temperature. This was $-.353 \pm .252$, the coefficient being 1.4

times the standard error and representing a percentage probability of occurrence of 84. This means that nesting begins earlier in May the higher the temperature and vice versa. An average night temperature for May of 52° F. (11° C.) appeared significant as only once did nesting begin earlier than May 25 when the night temperature averaged as low or lower than this and only once did nesting begin later than May 25 when it averaged higher.

FACTORS AFFECTING YEARLY LOSSES

The importance of yearly losses in affecting the abundance of the species has already been emphasized. The question now in order is the nature of the factors concerned in determining how much loss there will be.

The yearly loss was computed by determining the decrease in the combined number of adult and juvenal birds from one breeding season to the beginning of the next and determining what percentage of the total number present during the preceding breeding season this represented (Table 2).

TABLE 8. Factors affecting yearly losses.

Factor		Coefficient of correlation	Standard error	Coefficient divided by error	Percentage probability of occurrence
Average night temperature —	autumn	0	.....	....	..
	winter	—.425	± .247	1.7	91
	spring	—.358	± .263	1.4	84
	coldest month	—.115	± .298	0.4	*
Precipitation—	autumn	0	.....	....	..
	winter	0	.....	....	..
	spring	—.175	± .292	0.6	*
Relative humidity—	autumn	0	.....	....	..
	winter	0	.....	....	..
	spring	—.169	± .293	0.6	*

*Probably too low to be significant.

This percentage decrease had to be taken as representing the mortality or yearly loss of the species all through its breeding and wintering areas, since the exact route and wintering quarters of the particular individual birds under study are not known. Using these figures on percentage loss, correlations were attempted with various average climatic factors obtained from twelve uniformly spaced localities in the breeding range and five localities in the wintering range of the species (for localities see Kendeigh, 1934, Fig. 1). It was thought that if any correlations at all could be found they would have considerable significance since they would have to appear in spite of the uncertain nature of the loss index assumed for the entire species. Data for the breeding range were used only for September and May, all the rest being for the wintering range to approximate the time the species spends in each. Correlations were also made separately for each of the autumn (Sept.-Nov.), winter (Dec.-Feb.), and spring (March-May) seasons. The summer season receives special consideration beyond.

Table 8 indicates that temperature has probably a more profound influence upon yearly losses than any other factor investigated. This correlation is negative. The correlation during winter is a little higher than during the spring but undoubtedly both seasons are important.

Whether or not the percentage loss over winter was above or below the average appeared correlated with whether or not the average night temperature for the winter was above or below 52° F. (11° C.) or for the spring above or below 58° F. (14° C.). Apparently the average temperature for the entire season is of more importance than the temperature of any one month, even the coldest. Climatic conditions during the autumn months appear without significance. Relative humidity and precipitation show small negative correlations during the spring. These correlations are in the same direction and agree with the graphical correlation obtained in our earlier paper (Kendeigh, 1934). No correlation of any statistical significance was found with velocity of wind or with percentage possible daily sunshine.

Other factors besides climate cause losses in number of birds in any locality. During migration there may be some wandering of birds, particularly inexperienced young birds, into other regions. This should not seriously affect the abundance of the species in any locality, since it is balanced by birds wandering into the locality from other regions. Bird enemies, such as cats, black snakes, and red squirrels, may destroy some birds, particularly young birds during the summer. As discussed by Kendeigh, 1934, p. 302, such enemies became especially abundant during two periods in this study, 1925-1927 and 1931-1932. As these two periods are coincident with troughs in the curve of the bird's abundance, these enemies may have played a contributing rôle in the reduction of numbers, but no evidence is available that they were of primary importance. For instance, rodents were abundant in 1932, yet the bird had increased 30 percent in abundance by the beginning of the breeding season in 1933. No correlation was apparent between climatic factors during the summer and the abundance of the species the following year except as they affected the amount of reproduction.

The natural question arises as to the proportion of adults and immature that enter into the 72.8 percent decrease in total population from one breeding season to the next, and what the percentage of mortality is in adults and immature respectively. An attempt to answer these questions was made in an earlier publication (Kendeigh, 1934, p. 309), but the present estimates based on more detailed information now to be presented are probably more nearly correct.

Altogether from 1914 to 1934, approximately 9206 house wrens have been banded at this laboratory, of which 1831 were banded as adults and 7375 as nestlings. Out of this number there have been 783 returns recorded—631 of adults from the preceding year and 152 of nestlings. Excluding 1934, when the curtailment of trapping operations caused a diminution in the per-

centage of returns recorded, the average percentage of adults present during the years 1914 to 1932, inclusive, to return during the next year following is 29.0, while the average percentage of nestlings banded that return the following years amounts to only 2.5. Although this percentage of nestlings to return is small, it is of interest that of the total number of returns of all ages, these return nestlings make up 19.6 percent, a not insignificant proportion.

The maximum known ages of 907 birds banded during the years 1919 to 1929 rank as follows: 648—1.1 year old, 153—2 years, 66—3 years, 32—4 years, 6—5 years, and 2—6 years. All newly banded adult birds are considered young birds breeding for the first time. Where trapping of all birds is carried on year after year in the same locality, evidence has accumulated that new unbanded birds must have come in from surrounding districts. Ten recoveries of house wrens from outside the areas A, B, and C of intensive study (Table 1) were all first subsequent records of birds banded as nestlings. Of 39 birds that changed their nesting-sites during either the same or subsequent years between the three areas A, B, and C, 27 were young birds breeding for the first time and 12 were adults (3 males, 9 females). Some wandering of adult birds between these areas might be expected as they are not widely separated—in fact, area A actually lies within the boundaries of the larger area B, while portions of areas B and C are contiguous. The evidence is fairly convincing that the immature birds do practically all of the wandering into other regions and seeking of new areas in which to breed, while the adult birds almost invariably return to the immediate locality of their former breeding-sites. It is on this basis that all newly banded birds in the area of study are considered to have wandered in and to be nesting for the first time. If the omission of breeding during the first year after hatching by 12.2—17.9 percent of immature birds is taken into account, the average age of these newly banded birds is approximately 1.1 years. The average age of all 907 birds is approximately 1.5 years. This figure has been further substantiated by taking the average age of yearly breeding populations.

If the average longevity of adult birds is only 1.5 years, the average amount of mortality each year, assuming a constant average population level, must be the reciprocal of this (i.e., $\frac{1}{1.5}$), or 66.7 percent. Considering the number of birds in the different age classes mentioned above, the actual rates of loss in 1.1 year old birds during the subsequent succeeding years are 75.2, 16.0, 6.3, 2.0, 0.4, and 0.05 percentages respectively. If 66.7 percent of the adult birds perish before the advent of another season, and 29.0 percent are known to return the following year because they are recaptured, and 1.8 percent (which is 5.7 percent of total living population) presumably return the following year but are not recaptured until some later season, there remains unaccounted for only 2.5 percent of the adult population. This 2.5 percent may represent an error in the above calculations of average mortality or of the proportion that return or may be representative of a small fraction of

the adult population that drifts a short distance away from the intensive trapping area. That this unaccounted for fraction is so small would indicate that the above analysis is not far from correct. It is of interest in regard to banding technique that the banded return birds account for at least 92.5 percent of the probable survivors of the total adult population of the previous year.

Considering the years 1920 to 1934, but omitting the years 1926 to 1930, inclusive, because the rapid expansion during these years of trapping operations (see available boxes, Table 1) induced the capture of a disproportionate number of new birds, the average percentage of first year breeding birds (new birds and return nestlings) is 26.0 of the number of nestlings banded during the preceding years. The loss of 74.0 percent of the nestlings gives some index of the amount of mortality only if the drift of unbanded immature birds from surrounding districts into the trapping area is equal to the drift of banded immature birds outward. Very probably the drift outward of banded immature birds is greater because of the unusual concentration of breeding in the area, so the mortality rate is probably less than here indicated. A check is furnished on this rate of loss in young birds by comparing the ratio of adults to young at the end of the breeding season one year and the ratio at the beginning of the season the following year. These ratios are approximately 26.0: 74.0 percent and 27.4: 72.6 percent respectively, which represents only a slightly greater loss of young birds than of adults. The natural expectation would be that mortality of young birds, because of their inexperience and immaturity, would be greater than in adult birds, but as the above ratios are nearly similar and as the possible decrease in number of adults from the first to the second breeding season has already been shown to be very high (75.2 percent), it may well be that in this species the mortality of immature birds is not considerably above that of the adults. In order to account for the average loss in total number of birds (72.8 percent), the mortality rate in young birds may be considered as approximately 74 percent.

The 26.0 or more percent of the immature birds to survive consist of 2.5 percent that return and breed, of 0.5 percent that return but do not breed (which is 17.9 percent of total first year population in area), while of the remaining 23 percent an error of 2.5 percent may be allowed, as in the calculations for the adults, which would leave 20.5 percent that drift away into other regions. Return records of banded immature birds account for 11.5 percent or less of the probable living population of this group. The rest drift away and are with few exceptions never heard of again. It is of special interest that of the nestlings to return and breed in the same region of their birth, 62.9 percent are males and 37.1 percent are females. If the sex ratio of the nestlings involves more nearly equal numbers of males and females, then in the population that drifts out of the area the following year, the relative proportions of the two sexes must be reversed.

DISCUSSION

The number of factors affecting yearly fluctuations in abundance is considerable and so interacting as to make desirable some sort of classification. The simplest manner of grouping is into biological and climatic factors.

The biological factors of importance are mortality during the year, number of adults preceding year, amount of reproduction, local shiftings in surplus population, total number of broods per season, number of breeding females, percentage of total broods during first breeding period, number of broods per female, time of beginning to nest in spring, sex ratio, polygamy, and bird enemies. The first four of these factors act directly on yearly numbers of birds, the other factors all act indirectly through the first four.

It is desirable to think of climatic factors as not acting directly upon yearly abundance but only through one or another of the biological factors, although climate approaches closely to direct action through affecting mortality. The climatic factors of importance are average night temperature, precipitation, relative humidity, percentage possible daily sunshine, and velocity of wind.

It is difficult, perhaps impossible, to rank all of these factors in any regular order of relative importance. Probably any order of importance varies from year to year. Undoubtedly any one of the factors may under certain conditions be of considerable importance and several different factors are potentially able, when extreme, to be controlling. Therefore, only the following general comments will be made.

Of the four factors most directly concerned in controlling yearly abundance probably mortality, particularly during winter and spring, is more important than either the number of adults the preceding year, amount of reproduction, or local shiftings of population. This would seem to be true for several reasons. First, the coefficient of partial correlation obtained was the highest and most significant, particularly so over amount of reproduction. Secondly, the amount of reproduction as measured by the percentage increase during the breeding season is enormous, several times the possible accommodation if all individuals were to survive. Thus the relatively small yearly fluctuations that occur appear of lesser importance. Thirdly, the enormous potential increase in abundance due to reproduction would seem to more than compensate for variations in the number of adults at the beginning of the breeding season in spite of the fact that the amount of reproduction is determined in part by the number of these individuals. Lastly, the mortality is very high and subject to somewhat greater yearly fluctuation than the amount of reproduction. Relatively small variations in the mortality are potentially able to cause a considerable increase or decrease in the number of birds present during the following year. However, the mortality over winter and amount of reproduction are so nicely balanced that variations in either may

be important in causing a change in abundance the following year. The most important factor that affects mortality and amount of reproduction appears to be temperature. Thus the physiological resistance of passerine birds to low air temperature is of paramount significance in respect to variations in their yearly abundance.

The relative amount of resistance to low temperature in the two sexes is a matter of considerable importance and of theoretical interest not only in this but in all species and should be investigated. Differences in weight are frequently significant in indicating differences in resistance, but this may not always be true between the sexes because of differences in plumage and quality of endocrine activities. Endocrines would be particularly significant in their effect on metabolism, fat storage, and utilization of food. Differences in character of endocrine activities would seem most pronounced during the breeding season. Where the sexes have similar plumages and apparently more similar endocrine reactions, particularly during the non-breeding season such as during the critical winter period, differences in weight may have more significant and such differences in weight would be much more easily determined.

The relative amount of resistance of the two sexes to the same unfavorable environmental, particularly temperature, conditions may affect the readiness with which the species will recover from a drop in its abundance. If the male is less resistant than the female, during unfavorable years the sex ratio will be reduced, and the greater will be the difficulty experienced by each female in finding a mate. This will be offset, however, by the greater ease with which each male will obtain a mate, so that the amount of reproduction will be conditioned by the number of males. In species where the male is more resistant than the females, the sex ratio during unfavorable years will be increased, and the amount of reproduction will be determined by the number of females present. In either case the extent of recovery in numbers will be limited by the number of birds in the less resistant sex.

Other factors enter in. The relative tendency of the sexes either toward polygamy or polyandry is important. In species where the sex ratio is reduced during unfavorable years, the males may become polygamous and offset their diminished numbers so that actual recovery will be speeded. In species, where the sex ratio is increased, polyandry would similarly aid return to normal numbers but polyandry is believed to be less common than polygamy. It would seem therefore that a species with the male less resistant to unfavorable environmental conditions would recover more quickly from a loss of abundance and would maintain its abundance more uniform from year to year than would a species with the female less resistant.

The relation of breeding habits, i.e., polygamy and polyandry, to sex ratio and reproductive resiliency brings out another interesting point which is not new but which is frequently not fully appreciated. The mating rela-

tions of the sexes in different species are not fixed stereotyped phenomena. Breeding behavior is not exclusively an innate instinctive act but is flexible and subject to environmental influences. A species that is usually polygamous should not be considered as necessarily instinctively so, that is, its polygamous behavior is not necessarily due to inflexible nerve patterns. Rather the polygamous sexual relationships may be correlated with one-sided sex ratios. One may expect polygamy to occur in almost any species during certain years, given the proper circumstances. The same is only less true for polyandry, which is a less common phenomenon. As expressed in our earlier paper (Kendeigh, 1934) much of the behavior of an organism is based on, or the result of, the interplay between internal processes, such as the physiological, and environmental conditions. Here the physiological processes are the endocrine factors and other functions connected with the reproductive system, while the environmental conditions are such things as sex ratios. This concept, however, will not be carried further at this time.

The influence of climate, particularly temperature, upon the amount of reproduction is felt primarily through the number of broods started during the first breeding period and the extent to which this number is reduced or increased during the second breeding period. A word picture of this relationship is given on an earlier page. It appears that very low air temperature, especially at night, and very high daily maximum temperature are both unfavorable for starting broods. High air temperatures that are not extreme are well known to be depressing on the metabolism of homoiotherms while low air temperatures are generally stimulating. Recent evidence (Kleiber and Dougherty, 1934) indicates that high air temperature reduces energy intake (as food) more rapidly than it does body metabolism so that there would be under these conditions little energy available for mating and egg formation. With a drop to medial air temperatures, energy intake increases more rapidly than does metabolism so that a surplus becomes available that might go into mating and egg formation. At very low air temperatures, the rate of metabolism overtakes the increase in energy intake so that the amount available for mating and egg formation is again diminished. When the air temperature becomes sufficiently low, all the available energy must be used for maintenance of life itself. The whole question of mating, egg formation, number and size of broods, time of laying, etc., may be a matter of equilibrium between energy intake (as food) and energy outgo (for tolerance of low temperature, normal activities, etc.). When the latter approaches or equals the first, reproductive activities are curtailed; when a difference occurs, a surplus becomes available that can go into these functions. There may well be an optimum range of conditions somewhere between low night temperatures that unduly tax the energy outgo, as in early May, and daily maximum temperatures that unduly tax the energy intake, as in July. This explanation must for the present remain theoretical.

An analysis of the temperature records correlated with the reduction below average of the percentage of broods during the first breeding period, time of beginning to nest, and percentage mortality during winter and spring, indicates that critical conditions occur when the average night temperature becomes reduced to 52°-62° F. (11°-17° C.). These temperatures appear rather high because they are averages for periods of one month or longer and necessarily include records for nights when the air temperature does not fall very low. If these ineffective night temperatures were eliminated, the more critical night temperatures would lie somewhat lower.

The present study is not complete because many factors are not considered, such as food, disease, and also such climatic factors as intensity of sunshine and barometric pressure. Some of these factors cannot be studied yet because of lack of any quantitative information on their variations. At present, these other factors appear less important in this species than the ones that have been considered in this paper.

On the average, the non-breeding population in this species at any one time is roughly one-third of the total number of birds in the area, or, more exactly, somewhere between one-sixth and one-third during the first breeding period and between one-third and one-half during the second. Taking the season as a whole, the number of non-breeders is probably around one-tenth of the entire population. Young birds from previous years that have never nested greatly predominate in this non-breeding population, roughly around nine-tenths of the whole. Possibly males are more numerous than females.

Undoubtedly the size and constitution of the non-breeding population varies from year to year. Of factors that affect the size of the non-breeding population, the following may be considered: sex ratio, age, and weather conditions. There is no reason to believe that females may fail to breed because of a paucity of males. Usually there is an excess of males or the males become polygamous. Males may not breed, however, for lack of a sufficient number of females, as polyandry among females is poorly developed. Age of the young birds seems important as between 12.2 and 17.9 percent do not breed the first year after hatching. What differences may be involved between the first development of the gonads and the breeding instincts and their repeated development during each spring of succeeding years is not known. Finally, weather or climatic factors are effective, as during favorable years a larger proportion breed than during years when these factors are unfavorable.

The relation between breeding conditions and limiting factors in the species' distribution may well be considered. In our earlier paper (Kendeigh, 1934, p. 352), the importance of low night temperatures in limiting northward distribution of the house wren was emphasized. It was also pointed out that the average monthly night temperature correlated with the northern limits of the species' optimum range in the summer (about 60° F., 16° C.) is con-

siderably higher than the temperature correlated with the northern limits of the species' optimum range in the winter (about 50° F., 10° C.). The lower temperatures of the winter were also unfavorable combined with a greater number of hours of darkness. This discrepancy was explained partly by the lesser resistance of birds to low temperature in the summer over what it is in the winter due to loss in weight and feathers and also to the energy requirement during the summer for reproduction. It may well be that in winter the birds more nearly approach their potential limits of physical endurance than they do in the summer. In the summer, a surplus over and above that needed for mere existence must be reserved for the energy output required for carrying on reproduction. It seems, therefore, that northward distribution in the breeding season may be limited not by conditions unfavorable for existence alone but by conditions unfavorable for existence and reproduction. If energy is used for reproduction it then is unavailable for existence, so the existence factor is important in both winter and summer. The tolerance of low air temperature in the breeding season is, therefore, less than it is in the non-breeding season. It is of significance that the average night temperature for May, June, and July (62° F., 16.7° C.) below which the amount of breeding was reduced below average during some years on the area under investigation corresponds so closely to the temperature correlated with the northern limits of the species range. Actually, during only one year in this fifteen year period was the temperature reduced below 60° F. (16° C.).

A correlation may also be developed between high daily maximum temperatures unfavorable for breeding and the limits of the bird's southward distribution. Average daily maximum temperatures for July above 80° F. (27° C.) appeared unfavorable for initiating second broods in the area under study. This temperature limit cannot be fixed exactly, however, as a fair number of broods were started even with temperatures as high as 84° F. (29° C.). The southern geographic limits of the species' distribution are correlated with a mean daily maximum temperature during July of about 87° F. (31° C.), during June of about 85° F. (29° C.), and during May of about 77° F. (25° C.). Broods might well be started in southern regions during early May were it not that many birds are still in active migration, but during June and July the present data indicate that breeding conditions would be quite unfavorable for so doing. At high temperatures a premium is put on ability to curtail activity and energy transformation so as to avoid an undue increase in heat production and body temperature. The energy output required for reproductive activities is an added liability (Kendeigh, 1934, p. 332) that is avoided by limiting the distribution further to the north where temperatures do not get so high.

This paper should be considered a preliminary attempt at analyzing the problems presented. Very probably some revision will be required with the

accumulation of newer data. The paper should serve, if for nothing else, to point out the complexities of the relationships involved, the need for a more adequate and detailed knowledge of avian physiology, and the probable regulatory rôle of environmental influences.

SUMMARY AND CONCLUSIONS

1. A study was made of the factors affecting yearly fluctuations in abundance of a typical passerine bird (*Troglodytes aedon* Vieillot). The study was made by the statistical method involving the use of coefficients of correlation.

2. Over a period of 14 years on an area of approximately 15 acres, the following yearly averages were obtained: number of adults, 19.7; sex ratio, 109.6 males: 100 females; number of broods during first and second breeding periods, 7.8, 6.0; broods per female 1.5; percentage increase in number of birds during breeding season, 284; percentage of polygamous cases of breeding, 5.2; median date of starting to nest, May 25; and percentage annual mortality, 72.8.

3. Factors affecting yearly abundance are mortality, amount of reproduction, number of adults in preceding year, and local shifts of population, particularly of first year birds.

4. The amount of reproduction, figured as percentage increase in numbers during the breeding season, is determined by the total number of broods attempted, which in turn is controlled by the number of females present, by the relative number of broods attempted during the first breeding period, and by the number of broods per female.

5. The relative number of broods attempted during the first breeding period is affected principally by climatic factors during the breeding season, especially average night temperature, but also precipitation, wind velocity, and relative humidity. There is an indirect correlation with time of beginning to nest and a direct correlation with the size of the breeding population, particularly of females. The time of beginning to nest is affected by the average night temperature during May.

6. The number of broods attempted per female is affected by sex ratio and such climatic factors as average night temperature, percentage total possible daily sunshine, and wind velocity during the breeding season. Tendencies toward polygamy and polyandry are closely related to fluctuations in sex ratio and tend to compensate for variations in the latter.

7. Factors affecting amount of yearly mortality are average night temperatures during winter and spring, precipitation and relative humidity during the spring, and, to a lesser extent, predatory enemies.

8. A preliminary attempt at analysis of the non-breeding population indicates that it may amount to one-sixth to one-third of the total population during the first breeding period and one-third to one-half during the second

and that it is composed principally of immature birds but also contains some adults. An analysis of the rate of mortality over winter indicates that it is approximately 66.7 percent in adult birds and 74 percent in immature birds. Probably all living adult birds with few exceptions return to the same locality to nest year after year, but in immature birds there is a tendency for dispersal amounting to about 20.5 percent of the number leaving the nest. Only about 3.0 percent of the immature birds return to the locality of their birth, but this represents about 11.5 percent of the number alive at that time.

9. Certain theoretical aspects of breeding behavior, relative importance of various biological and climatic factors, physiological bases of climatic influences, and potentialities of recovery from unfavorable years are discussed.

10. Energy requirements for reproduction reduce the tolerance of birds to low and high air temperatures so that the rôle of air temperature in determining the northern and southern limits of the breeding distribution of the species is exerted by producing conditions unfavorable not only for survival but for survival and reproduction.

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PERPETUATION OF SPRUCE ON CUT-OVER AND BURNED LANDS IN THE HIGHER SOUTHERN APPALACHIAN MOUNTAINS

By

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PERPETUATION OF SPRUCE ON CUT-OVER AND BURNED LANDS IN THE HIGHER SOUTHERN APPALACHIAN MOUNTAINS

INTRODUCTION

Reduced to a fragment of its former expanse, the spruce forest of the Southern Appalachian Mountains in West Virginia, Virginia, Tennessee, and North Carolina possesses an interest and importance wholly disproportionate to the area it now occupies. It is a southern extension of the northern spruce forest which for a long time has been the mainstay of the paper industry as well as a source of valuable lumber. In the Southern Appalachians, where spruce forest is found only in the cool climate of the loftiest peaks and ridges, its commercial value is equaled, if not exceeded, by its value as a protection for watersheds in holding the shallow soil to the steep, wet slopes, as a check on the silting up of reservoirs, as a refuge for wild life of many kinds, and as a unique scenic attraction in a region of growing recreational appeal. Furthermore, it provides wilderness or natural areas where the interactions of the various plants and animals comprising the forest community may be observed and studied under undisturbed natural conditions.

The usefulness of spruce, both for saw timber and for pulpwood, has resulted in large-scale exploitation, followed generally by fire and leading to to the virtual destruction of the forest. At present, out of an original area of virgin spruce forest estimated at 1 million acres, less than one-tenth remains, of which about 50,000 acres is under Federal and State ownership and a considerably smaller area is privately owned.

In recognition of the urgency of preserving what is left of the spruce forest and of restoring it, so far as possible, where it has been destroyed, a study was undertaken by the writer of virgin, cut-over, and burned spruce lands for the purpose of obtaining information on: (1) The conditions prevailing on such lands in different states of productivity; (2) the reproduction characteristics of spruce; (3) the obstacles to reproduction; and (4) the measures by which the spruce forest may be restored and perpetuated.

THE SPRUCE FOREST IN ITS SOUTHERN HABITAT

The red spruce *(Picea rubra)* which characterizes and gives its name to the spruce forest of the Southern Appalachians is identical with the red spruce of the Northeast. Its most characteristic associate in North Carolina and Tennessee (but not in West Virginia) is the southern balsam fir *(Abies fraseri)*, corresponding to the balsam fir *(A. balsamea)* of the Northeast. Within the Southern Appalachian region the range of these two species is limited to a relatively small area high enough to have the cool climate found

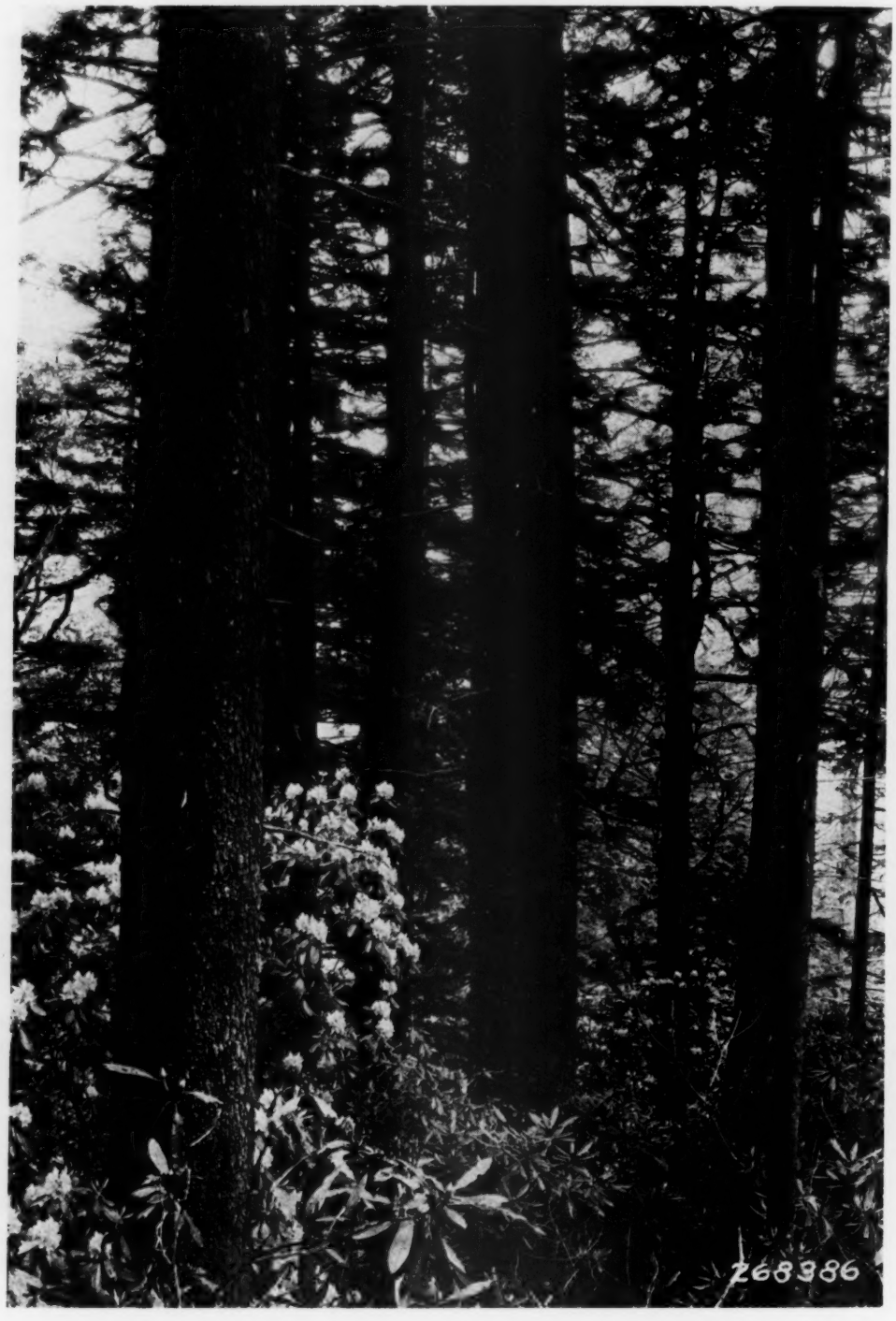


FIG. 1. Virgin spruce forest in the Black Mountain natural area, Pisgah National Forest, North Carolina. The shrubs are *Rhododendron catawbiense*.

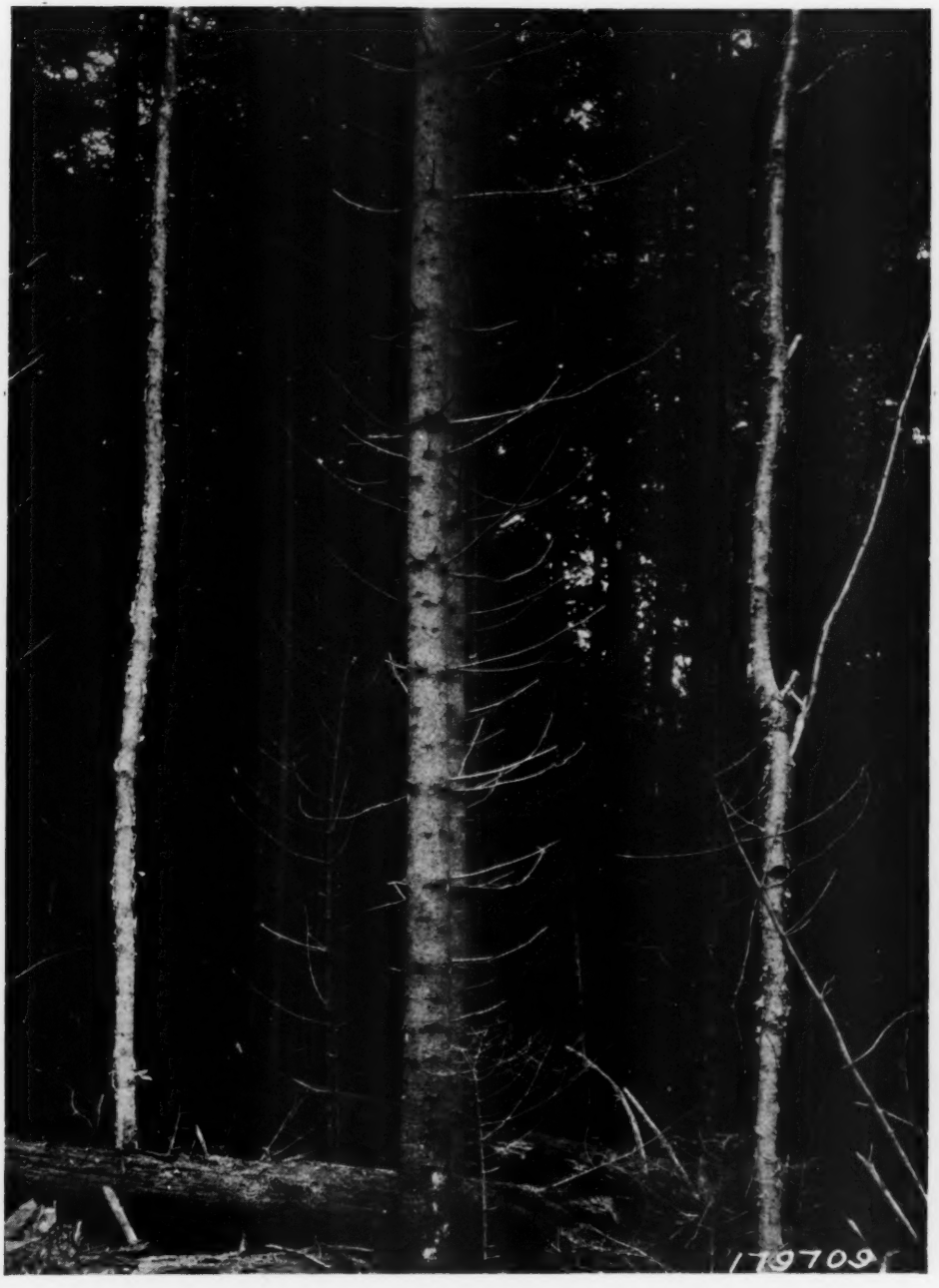


FIG. 2. Young pole stand of second-growth red spruce on a thin-soiled ridge top on Cheat Mountain, Randolph County, West Virginia.

at lower elevations in the North. They occur on slopes and summits above 3,500 feet in the Allegheny highlands of West Virginia, and above 4,500 feet in the mountains of Tennessee and North Carolina (figs. 1 and 2). While these elevations have temperatures comparable to those of southern New England, the atmosphere is more humid and the rainfall heavier, especially dur-

ing the growing season. Consequently the red spruce attains its maximum development in this region, growing more rapidly and attaining larger size than in the Northeast (Dana, 1930; Murphy, 1917; Westveld, 1930). According to Verne Rhoades, formerly Executive Secretary, North Carolina Park Commission, a detailed cruise of 20,000 acres of unburned virgin spruce in the Great Smoky Mountains showed an average of 35 trees to the acre having a diameter of 8 inches or more, containing an average of 25 to 30 cords to the acre when 6-inch trees were included. Red spruce in these mountains is known to have reached an age of 300 years, a diameter of 57 inches at breast height, and a height of 162 feet, many trees being found that exceeded 100 feet in height.

In North Carolina and Tennessee the range of the southern balsam fir generally is the same as that of spruce. Localities exist where fir does not accompany spruce, but as a rule it constitutes an abundant associate. This is particularly true at the highest altitudes, where it also forms almost pure stands of small extent. Spruce predominates at the intermediate elevations as well as on very wet or unusually thin soils. There it often grows in pure or almost pure stands. But the spruce belt of the Southern Appalachians contains very little of the spruce flat or spruce swamp land so frequently encountered in the North.

Table 1 shows the composition of typical unburned virgin spruce forest in the Southern Appalachians of Tennessee and North Carolina, and of unburned virgin and second-growth spruce in the Allegheny highlands of West Virginia. The data used for this table, as well as for those that follow, were obtained by the Appalachian Forest Experiment Station of the United States Forest Service from 55 representative areas in West Virginia, Virginia, Tennessee, and North Carolina. On most of these areas counts were made of all trees and of tree reproduction by species and size classes. On account of the density of some stands and the need for close examination to reveal the smaller growth, the reproduction counts were made on strips 10 to 20 feet wide, while the larger trees were tallied on strips 0.5 to 1 chain in width. The survey covered different conditions, slopes, and exposures.

In the lower part of the spruce zone and on deep rich soil, the eastern hemlock *(Tsuga canadensis)* and hardwoods, particularly yellow birch *(Betula lutea)*, mingle with the spruce. Other hardwoods in mixture with the spruce are beech *(Fagus grandifolia)*, sweet birch *(Betula lenta)*, sugar maple *(Acer saccharum)*, red maple *(A. rubrum)*, and black cherry *(Prunus serotina)*. Small tree species associated with the spruce and fir in the Southern Appalachians are pin cherry *(Prunus pennsylvanica)*, mountain maple *(Acer spicatum)*, striped maple *(Acer pennsylvanicum)*, mountain ash *(Sorbus americana)* mountain holly *(Ilex montana)*, serviceberry *(Amelanchier canadensis)*, and dogwoods *(Cornus florida* and *C. alternifolia)*. Shrubs, consisting chiefly of rhododendrons, *(Rhododendron catawbiense* and

TABLE 1. Composition (number of trees per acre) of unburned virgin and second-growth spruce forest in the Southern Appalachian region.

Diameter breast high (Inches)	Virgin stand, Black Mountains, Yancey County, N. C.[1]			Virgin stand, Pisgah Ridge, Transylvania County, N. C.[2]			Virgin stand, Unaka Mt., Unicoi County, Tenn.[2]		Virgin stand, Turkey Run, Tucker County, W. Va.[3]			Second-growth stand following clear cutting during Civil War, Cheat Mt., Randolph County, W. Va.[3]	
	Red spruce	Southern balsam fir	Yellow birch	Red spruce	Southern balsam fir	Commercial hardwoods[4]	Red spruce	Commercial hardwoods[5]	Red spruce	Eastern hemlock	Commercial hardwoods[6]	Red spruce	Commercial hardwoods[7]
Less than 1	..	..	..	217	141	300	323	..	900	406	..	732	...
1	3	0	6	29	12	23	146	6	12	4	44	231	168
2	7	4	4	29	12	24	144	10	4	2	44	121	163
3	4	4	6	11	7	8	79	5	4	..	12	40	105
4	6	3	3	8	14	11	67	9	30	..	26	17	95
5	6	3	8	5	10	12	20	5	40	..	16	11	69
6	6	4	2	6	6	13	30	3	76	..	4	14	54
7	5	2	1	1	3	1	8	1	34	..	..	2	27
8	8	2	4	8	5	7	25	3	88	..	4	4	20
9–10	6	3	4	8	6	3	11	..	120	..	..	2	15
11–12	9	3	6	4	7	4	14	..	54	..	2	4	7
13–14	7	2	6	5	3	2	10	1	12	8	..	2	5
15–16	4	..	1	1	1	1	16	2	8	4	2	...	...
17–18	6	..	4	3	2	..	14	3	..	2	..	1	...
19–20	3	..	1	2	..	..	13	1	2	..	..	...	1
21–24	9	..	2	8	2	6	18	1	..	..	2	...	...
25–28	8	..	1	2	..	..	2	..	2	..	..	...	...
29–32	5	..	..	1	..	..	..	..	..	..	..	...	...
33–38	3	..	..	3	..	1	1	2	..	..	..	...	...
TOTAL.....	105	30	59	351	231	416	941	52	1386	426	156	1181	729

[1]Based on 4 sample plots aggregating 1.4 acres, tallied by L. I. Barrett.
[2]Based on 1 acre of strip tally.
[3]Based on 0.5 acre of strip tally.
[4]Beech 91.8 percent, yellow birch 7.2 percent, and buckeye 1.0 percent. Also there were 3 eastern hemlock saplings less than 1 inch d.b.h. and 863 small tree species and tall shrubs all under 11 inches d.b.h. composed of rhododendron 77.2 percent, mountain maple 11.9 percent, striped maple 4.1 percent, and small quantities of mountain holly, mountain laurel, serviceberry, pin cherry, mountain ash, and dogwood.
[5]Yellow birch 61.5 percent, beech 34.6 percent, and black cherry 3.9 percent. Also there were 134 small tree species and tall shrubs all under 8 inches d.b.h. composed of mountain maple 37.3 percent, mountain holly 20.9 percent, mountain ash 9.0 percent, and small quantities of serviceberry, pin cherry, striped maple, and huckleberry.
[6]Yellow birch 74.4 percent, sweet birch 14.1 percent, red maple 6.4 percent, and black cherry 1.3 percent, and a small amount of beech. Also there were small tree species and tall shrubs as follows: mountain holly 16, pin cherry 8, serviceberry 4, and witch hazel 4, all under 9 inches d.b.h.
[7]Yellow birch 56 percent, beech 27 percent, red maple 14 percent, and small quantities of sugar maple, black cherry, and cucumber. Also there were 133 small tree species and tall shrubs all under 9 inches d.b.h. composed of serviceberry 51.9 percent, mountain holly 24.8 percent, pin cherry11.3 percent, mountain maple 9.8 percent and small quantities of dogwood and striped maple.

R. maximum), mountain laurel *(Kalmia latifolia)*, huckleberries (*Vaccinium* spp.) witch hobble and other viburnums (*Viburnum* spp.), willows (*Salix* spp.), currents (*Ribes* spp.) and gooseberries (*Grossularia* spp.) frequently form a dense undergrowth. Rhododendron sometimes occurs as a very dense, practically pure understory.

On account of their thin bark, the resinous exudations commonly occurring on it, the shallow root system, and the slow early growth which delays the formation of a protective corky layer in the bark (Murphy, 1917), isolated specimens of the red spruce are highly susceptible to injury from fire. And by the long persistence of their lower branches, they are more

exposed to complete destruction than their associate species which have higher crown bases. When a ground fire consumes the litter covering the superficial root system of the spruce, the roots are almost certain to be severely injured, particularly on thin soil. The fire may not be hot enough to scorch the trunk, but the roots suffer both from the fire and from the resulting desiccation. Even if the tree is not killed outright, its roothold is so weakened that it becomes an easy victim of windthrow.

The natural spruce forest is very dense, with a moist, moss-covered floor. The air within it is usually so humid, the moss and litter so moist, the decay of fallen timber so rapid, and the rotting wood so wet and soggy, that, in spite of the inflammability of the individual trees, the forest as a whole is nearly immune to fire except in seasons of excessive dryness or in cases when the forest cover has been broken by cutting, windfall, or other causes. Undisturbed spruce forests on ridge crests are known in several instances to have stopped fires that swept up cut-over slopes below. When, as happens in rare instances, the litter of the natural forest has become dry enough to burn, the likelihood is that a fire will kill the entire stand, either by destroying it immediately or, where the trunks and crowns escape injury, by exposing the surface roots.

MAJOR FACTORS INFLUENCING NATURAL REPRODUCTION

Red spruce, the most valuable of the several species found in the spruce forest, is the most difficult to reproduce naturally. Among the variable natural factors influencing its reproduction, three call for special consideration, namely, seed supply, soil and moisture, and competing vegetation.

SEED SUPPLY

The age at which spruce begins to bear seed of good quality depends on soil and moisture conditions, exposure to wind and sun, and the amount of light received by the crown. In the forest it begins to bear seed when the crown reaches direct light, but it does not bear heavily until the top of the crown thickens. In the open, and under favorable conditions of soil, moisture, light, and exposure, seed production begins as early as the fifteenth to twentieth year, and heavy crops follow by the thirtieth to thirty-fifth year. In dense, even-aged second growth, full seed crops are rarely produced until the stands reach an age of 40 to 50 years. Spruce continues to bear seed up to an advanced age.

Observations have not been made over a sufficiently long period to determine with any degree of certainty the frequency and abundance of seed production by spruce. It may bear a small amount of seed annually, and under favorable conditions good crops may occur in two successive years. The intervals between full crops, however, vary generally from 3 to 6 or 7 years. The seed is 60 to 80 percent viable, and the viability is retained for

at least 2 years under ordinary conditions of storage, while under favorable conditions it may be preserved much longer. In a poor seed year not only are there fewer seeds, but the seeds are of poorer quality. In the Southern Appalachian region the cones of the red spruce mature as a rule during the first half of October, but the exact time depends on climatic conditions. Hot and dry weather hastens maturity, while cool and damp weather retards it. When fully mature, the cones open and most of the seeds fall out, though a few remain in the cones during the winter.

The seeds are well adapted for distribution by the wind, and owing to their small size, light weight, and relatively large wings, are often carried considerable distances. The extent of dispersal depends on the height of the tree and the velocity of the wind. In a measure, of course, the flight of the seed will be influenced by convectional air currents; but knowing the average wind conditions during dissemination and the rate at which the seeds fall through still air, it becomes possible to determine the probable distance to which they will be carried. Red spruce seeds fall about 4 feet per second in still air (Siggins, 1933). The seed-fall rate in still air of southern balsam fir and yellow birch—two common profilic associates of the red spruce—was found to be about 5 feet per second. The importance of the wings in increasing the buoyancy of the seeds is emphasized by these figures. The red spruce seeds, averaging about 139,200 per pound, fall more slowly than either those of yellow birch, averaging 394,600, or those of southern balsam fir, with an average of 44,000 to the pound. The number of feet seed will travel horizontally equals the number of seconds required for the fall from its place on the tree multiplied by 1.47 times the velocity of the prevailing wind in miles per hour.[2]

All the seeds do not fall at the same rate and the combinations of tree heights and wind velocities are numerous, but the influence of height and wind velocity on the distances over which the seeds of red spruce, yellow birch, and southern balsam fir are carried may be shown by a few examples. If seeds of these species are released at a height of 50 feet in a 5-mile wind, 50 percent of the spruce seed will fall within 960 feet of the starting point, and 90 percent within 1,200 feet, while 50 percent of the birch and fir seed will fall within 700 feet, and 90 percent within 820 feet. From a height of 100 feet, with a 13.5-mile wind, one-half of the red spruce seed will fall within 1 mile of the tree, while the seed of southern balsam fir or yellow birch would require a 19-mile wind to be carried equally far. These figures are conservative, since they apply only to horizontal distances and do not take into account convectional air currents. Since much of the Southern Appalachian spruce forest occurs on the higher mountain slopes and ridges and seed released from such locations travel much farther than in level country, it is evident that whatever spruce seed is produced may be widely scattered (fig. 3).

[2] A wind having a velocity of 1 mile per hour blows 1.47 feet per second.

FIG. 3. A strip of uncut spruce and fir timber on the main crest of the Black Mountains (North Carolina) capable of disseminating seed great distances down the mountain sides.

SOIL AND MOISTURE CONDITIONS

In the Southern Appalachians the soil on high slopes and ridges, where most of the spruce forest occurs, is generally thin and rocky, varying from sandy loam to clay loam. The best of the spruce grows on the deeper of the sandy loams found on moist but well-drained slopes and benches. The forest floor is usually a carpet of moss and upland peat, which sometimes has practically no mineral soil beneath it but rests directly on the rocks. Such a more or less spongy layer in which the spruce has its roots may be a foot thick, and frequently it is highly acid. This acidity delays the decomposition of the peat and the incorporation of humus into the soil.

Red spruce seed germinates well on mineral soil, moss, peat, decaying wood (stumps and logs), and even on litter that is sufficiently moist. When seeds germinate on surface litter, the seedlings usually perish during the first period of dry weather. The moss and peat, on the other hand, commonly remain damp, and the appearance of moss on the forest floor indicates a sufficiency of moisture to make germination possible throughout the growing season.

That greatest obstacle to natural reforestation is the desiccation of this layer of moss and peat after cutting, or its destruction by fire, followed by the surface drying of the mineral soil. The best means of preserving adequate

moisture for the establishment of seedlings is probably found in the method of partial cutting, to which reference will be made later.

COMPETING VEGETATION

As a rule, the reproduction on cut-over areas in the spruce forest consists largely of hardwood species, with more seedlings of southern balsam fir than of spruce. The relative scarcity of spruce seedlings on large clearings as well as in small openings in the forest cover may be attributed in a great measure to the long intervals between full seed crops of spruce in comparison with those between fir seed crops and with the usually abundant annual production of the hardwoods. The spruce reproduction is not only outnumbered but is also outgrown by other species—herbs, shrubs, and trees—during the first few years; the hardwood tree species in particular maintain this advantage. In mixed stands of spruce and hardwoods the failure of spruce reproduction may further be attributed to the litter of hardwood leaves covering the ground at the time of spruce seed dispersal. These leaves dry out soon after being shed, becoming tough and impenetrable to the roots of spruce seedlings germinating above them and preventing the seedlings from becoming established in the mineral soil below.

The occurrence of pure stands of spruce may be traced to the ability of this species to maintain itself on sites unfavorable to its competitors. On the thin soil of the steep mountain slopes, or on soil that is wet, the competition of the hardwoods is reduced because of inability to adapt their root systems to such soils. Therefore spruce is more abundant, not where the best conditions for its growth exist, but where its competitors are less able to grow.

CONDITIONS ON LOGGED, UNBURNED SPRUCE LANDS

TYPES OF LOGGING AND THEIR IMMEDIATE EFFECT ON THE STAND

The present condition of the cut-over spruce lands is the result of a variety of logging methods. A common practice has been to remove saw timber by railroad, supplemented either with ground or overhead steam skidding or with animal skidding. Ground skidding was generally combined with the use of animals to increase its range of operation. Spruce pulpwood originally was taken out chiefly by steam or by animal power alone. More recently it has been moved to the railroad or motor truck road by animal skidding combined with fluming or "ballhooting" (rolling or sliding the logs down a steep mountain side, a method obviously destructive of reproduction).

Any method of logging destroys some reproduction, but steam skidding results in more damage to the residual stand than any other method. Where this method of skidding was used a large proportion of the small trees were broken and scattered among the slash (figs. 4 and 5). Moreover, a significant

FIG. 4. Heavy cutting and steam-skidder logging wrecks the forest and leaves a veritable firetrap of slash and logging debris. *A*, all living trees in the skidding lanes and adjacent to the skidder were destroyed, leaving only a few small clumps of young growth near the "tail" trees to which the skidding cable block was attached; *B*, residual stand after removal of saw timber.

FIG. 5. Cut-over spruce land following removal of conifers for timber and pulpwood. No timber of merchantable size left except a few hardwoods.

proportion of the reproduction, as well as larger trees not otherwise destroyed, were uprooted so that very little young growth remained after the skidder operations. Slash and other logging débris also accumulated between the skidder lanes and often covered much of the advance growth not actually destroyed. Only on areas lacking young growth can the forest possibly benefit from steam skidding, which through tearing up the ground and removing the surface litter, exposes the mineral soil and thus prepares a good seed bed for the establishment of spruce reproduction, unless excessive erosion of the soil follows. Machine logging of this type, so common in the southern spruce forest 15 to 20 years ago, probably will not be practiced again in the small remaining vestiges of spruce timber.

Areas logged by horses or oxen were found to have suffered much less injury than steam-logged areas, and the trees remaining were more uniformly distributed. On these areas only about 10 to 15 percent of the advance growth was destroyed by the operations. This compares favorably with the degree of damage on horse-logged areas in New England (Westveld, 1926).

Fluming was found to have caused less damage than any other method to both the "hold-overs" and the advance reproduction.

NATURAL RECOVERY AFTER LOGGING

The character of the stand remaining after cutting varies with the logging practice, the composition of the original forest, and the severity of the

cut. The present stand consists of the residual advance reproduction, the hold-overs left at the time of logging, and the new reproduction established after the cutting. The composition of the present stand on typical unburned spruce lands cut over from 1 to 35 years prior to examination is shown in table 2. The more important deductions from the observations on the nat-

TABLE 2. Composition (number of trees per acre) of present stand on cut-over but unburned spruce lands.

Period since cutting and species in present stand[1]	Diameter breast high (inches)			
	Less than 1	1 - 4	5 - 12	More than 12
Cut-over 1 year:[2]				
Red spruce	173	9	5	0
Southern balsam fir	319	26	16	1
Commercial hardwoods (yellow birch)	91	2	1	1
Small trees and tall shrubs (pin cherry, rhododendron)	22,761	89	1	0
Cut-over 3 years:[3]				
Red spruce	88	13	2	0
Southern balsam fir	555	363	80	0
Eastern hemlock	27	0	0	0
Commercial hardwoods (yellow birch)	715	2	2	2
Small trees and tall shrubs (pin cherry, mountain maple, rhododendron)	5,418	175	9	0
Cut-over 5 years:[4]				
Red spruce	2,861	182	30	0
Southern balsam fir	1,201	251	43	0
Commercial hardwoods (yellow birch)	...	3	3	0
Samall trees and tall shrubs (rhododendron)	...	1,317	0	0
Cut-over 6 years:[5]				
Red spruce	467	20	5	0
Southern balsam fir	4	1	1	0
Eastern hemlock	165	8	1	1
Commercial hardwoods (yellow birch)	21,543	51	40	15
Small trees and tall shrubs (rhododendron, pin cherry)	32,421	3,430	7	0
Cut-over 11 years:[6]				
Red spruce	175	155	43	1
Commercial hardwoods (yellow birch)	396	179	19	38
Small trees and tall shrubs (rhododendron, viburnum, mountain maple, pin cherry, mountain holly)	4,396	1,572	3	0
Cut-over 13 years:[7]				
Red spruce	253	210	60	8
Southern balsam fir	122	84	35	2
Eastern hemlock	14	1	0	0
Commercial hardwoods (yellow birch, beech)	3,597	146	44	35
Small trees and tall shrubs (rhododendron, mountain maple, serviceberry, striped maple, mountain holly, pin cherry)	3,702	229	21	2

[1]Species in parentheses following "Commercial hardwoods" and "Small trees and tall shrubs" constitute approximately 90 percent of these groups.
[2]Based on 3.2 acres of strip tally on Pigeon River watershed, Haywood County, N. C.
[3]Based on 0.9 acre of strip tally, in upper portion of type, Hornbuckle Creek, Jackson County, N. C.
[4]Cut-over for pulpwood 5 years before and again immediately prior to examination. Based on 0.3 acre of strip tally on Pigeon River watershed, Haywood County, N. C.
[5]Based on 1.7 acres of strip tally, in lower portion of type, Pigeon River watershed, Haywood County, N. C.
[6]Based on 0.7 acre of strip tally on Unaka Mountain, Unicoi County, Tenn.
[7]Based on 1.7 acres of strip tally on Plott Balsam Mountains, Haywood and Jackson Counties, N. C.

TABLE 2. Composition (number of trees per acre) of present stand on cut-over but unburned spruce lands. (Continued)

Period since cutting and species in present stand[1]	Diameter breast high (inches)			
	Less than 1	1 – 4	5 – 12	More than 12
Cut-over 17 years and again 1 year:[8]				
Red spruce	2,602	244	154	2
Commercial hardwoods (yellow birch)	...	598	24	4
Small trees and tall shrubs (mountain holly, pin cherry)	...	58	2	0
Cut-over 17 to 20 years:[9]				
Red spruce	481	250	79	3
Eastern hemlock	50	8	3	1
Commercial hardwoods (yellow birch, beech, red maple)	...	986	52	15
Small trees and tall shrubs (mountain maple, pin cherry, striped maple, serviceberry, mountain ash, mountain holly)	...	276	16	0
Cut-over 35 years:[10]				
Red spruce	196	114	81	17
Eastern hemlock	1	0	0	0
Commercial hardwoods (yellow birch, beech)	...	664	102	27
Small trees and tall shrubs (rhododendron, mountain maple, pin cherry)	...	130	10	0

[8]Based on 0.5 acre of strip tally on Cheat Mountain, Randolph County, W. Va.
[9]Based on 12.2 acres of strip tally on Otter Creek and Shavers Fork of Cheat River watersheds, Randolph and Pocahontas Counties, W. Va.
[10]Based on 2.7 acres of strip tally on Cheat Mountain, Randolph County, W. Va.

ural recovery of unburned cut-over spruce lands pertain to (1) the nucleus of softwoods left after cutting, (2) the predominance of advance growth, (3) the ultimate dominance of hardwoods when left standing, and (4) the tendency of hardwood tree reproduction and shrubs to monopolize cut-over areas by out-numbering and out-growing the conifers. It is evident that a nucleus of conifers remained after cutting on practically all the unburned cut-over lands (fig. 4, B), although many years must elapse before the stand will contain anything like the original proportion of large conifers.

The studies on cut-over areas, as well as observations in uncut stands, indicate that generally most of the red spruce and southern balsam fir reproduction found on areas recently cut over was present in the stand at the time of cutting and commonly represents the accumulation of seedlings and saplings over several decades. Since the growth rate of seedlings is relative to the amount of light and moisture they receive, forest-grown seedlings of the same size may differ widely in age. After a stand is cut it is often impossible to distinguish positively between advance reproduction and subsequent new growth except by cutting the seedlings and ascertaining their age by a count of the annual rings. Figure 6, which is based upon such counts made on a typical spruce site, compares the height growth of advance spruce reproduction, released and overtopped, with that of open-grown reproduction.

The tendency of spruce to replace itself on unburned areas of thin, wet

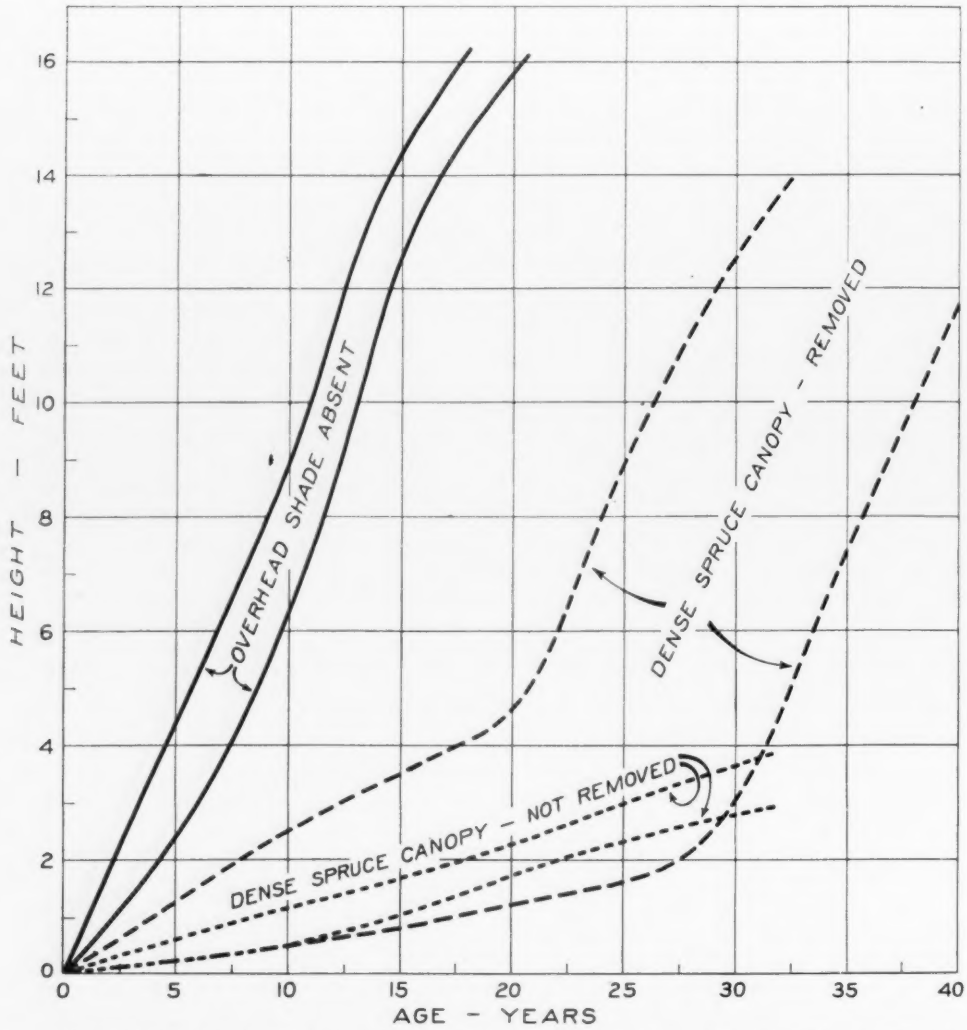


FIG. 6. Relative height growth of typical red spruce seedlings under different cover conditions. Tucker County, West Virginia.

soil, even after relatively heavy cutting (fig. 7), is not so marked on the deeper, better-drained soils, where, as has already been mentioned, the proportion of spruce and fir reproduction that comes in after heavy logging, especially when all merchantable pulpwood is removed, is diminished through the encroachment of aggressive hardwoods. Observations on areas where hardwood and spruce reproduction had an even start indicate that the hardwoods, due to their more rapid early growth, soon outstrip and completely overtop the conifers (fig. 8). Because of their tolerance of heavy shade, the conifers are capable of persisting for many years when overtopped, but under such conditions they develop short, umbrella-shaped crowns and often grow only an inch or two in height each year.

Spruce, however, possesses a marked capacity for recovery after sup-

FIG. 7. Red spruce reproduction on thin, wet soil from which practically all merchantable spruce was removed in one cutting. Randolph County, West Virginia.

pression. Trees suppressed for half a century or more may develop to merchantable size after being released. Most advance spruce reproduction that has not been suppressed too long or overtopped too soon by hardwoods will respond to release with a growth rate often approaching that of free-growing seedlings. On the poorer lands, the conifers, after a severe struggle, push their way through the stand of young hardwoods and assume a dominant position in the crown canopy. On the better sites, however, the hardwoods usually dominate until they are mature; the conifers dominate only after the hardwoods die out of the stand.

The character of the stand within a year after a pulpwood cutting is illustrated by the first example in table 2. This was a representative western North Carolina operation, in which the saw timber was removed by combined steam and animal skidding. After logging, the pulpwood was cut from the smaller trees as well as from the tops of the larger trees cut for sawlogs. The table indicates clearly that the scattered residual stand of spruce and fir and advance reproduction is inadequate to form a satisfactory new stand, and that this must depend chiefly on new reproduction by seed from the larger trees. The stand would have been in much better condition for restocking if pulpwood cutting had not followed the removal of the saw timber, or if, at least, more trees of pulpwood size (5 to 12 inches d.b.h.) had been left (fig. 5).

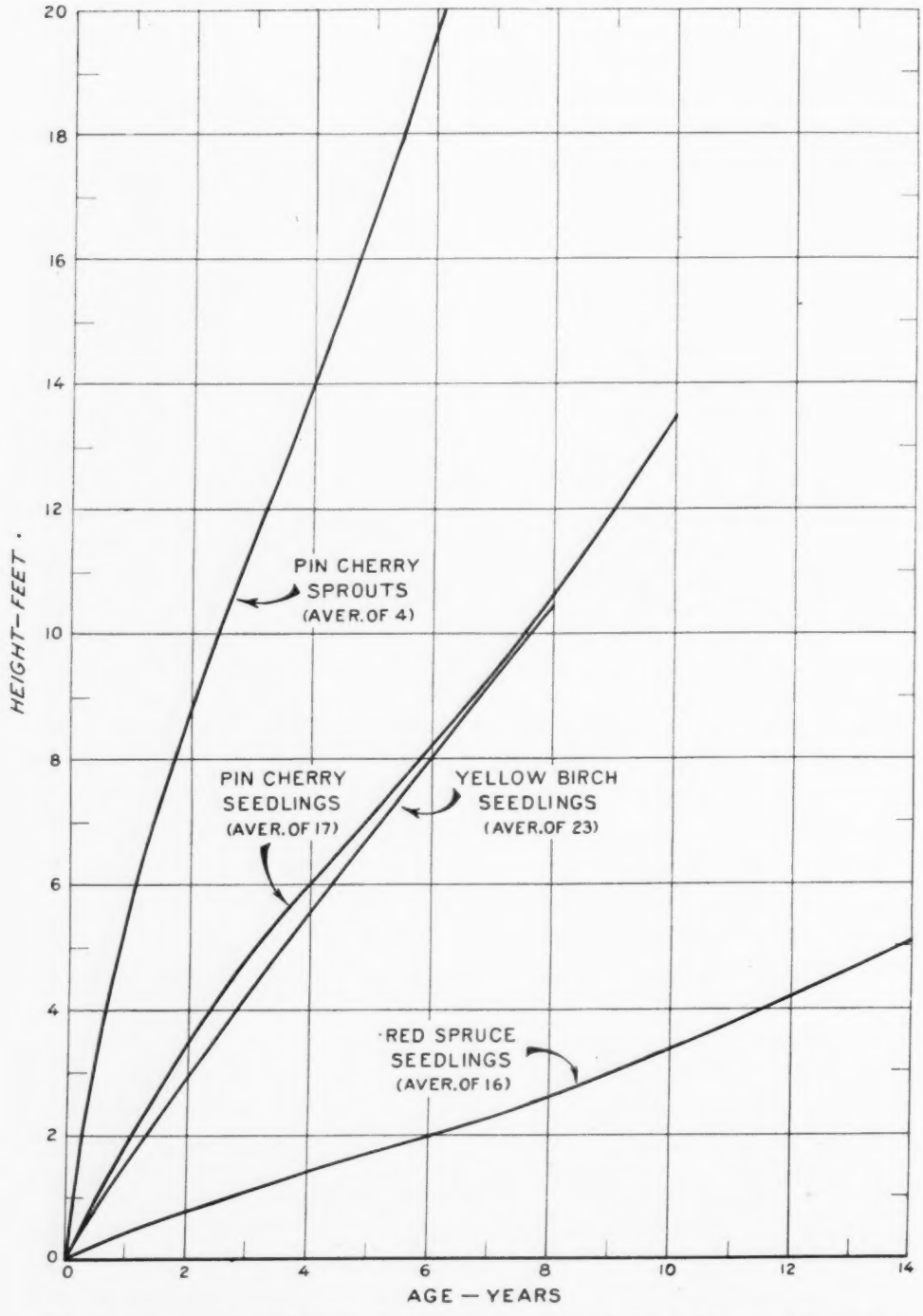


FIG. 8. Comparative height growth of red spruce and yellow birch seedlings and pin cherry seedlings and sprouts on burned spruce land. Unaka Mountain, Unicoi County, Tennessee.

GROWTH OF TREES LEFT AFTER LOGGING

Figures 9, 10, and 11 give the diameter growth of the spruce released by cutting on two areas in Pocahontas and Randolph Counties, W. Va., 22 years and 35 years after cutting, respectively. Table 3 gives an analysis of the growth on the latter area. The results of another study, made on an area in Tucker County, W. Va., 17 years after cutting, are shown in table 4. The comparative growth rates in the tables and figures are expressed in terms of basal area at breast height. It is evident from these data that increase in growth rate of the residual stand following cutting varies widely with the extent to which the trees have remained free since cutting and also with the size and condition of the trees at the time of release.

TABLE 3. Diameter growth of red spruce after removal of largest trees 35 years before measurement (Cheat River watershed, Pocahontas and Randolph Counties, W. Va.)

Average diameter[1] at time of cutting	Average diameter[1] 35 years after cutting	Average diameter[1] 35 years after cutting if original growth rate had continued	Increase in rate of average annual growth in basal area as result of cutting	Average annual diameter growth		Average time elapsing before increased growth began	Basis
				For decade before increased growth began	During period of increased growth		
Inches	*Inches*	*Inches*	*Percent*	*Inches*	*Inches*	*Years*	*No. of trees*
RELEASED TREES REMAINING FREE SINCE CUTTING							
1.2	9.1	3.1	141.8	0.04	0.24	2.3	6
2.1	10.2	4.1	54.6	.05	.24	2.5	24
3.2	10.7	5.2	24.5	.05	.24	3.1	22
4.1	11.0	5.4	15.3	.03	.20	3.2	18
5.0	12.3	7.3	11.2	.06	.22	3.2	17
6.1	12.2	7.8	6.7	.04	.18	3.8	20
7.1	13.2	9.0	5.3	.05	.19	3.5	23
8.2	14.1	10.3	4.0	.06	.18	3.8	12
8.9	14.4	10.8	3.2	.05	.17	3.3	17
10.0	14.9	11.3	2.7	.03	.17	4.6	5
10.9	15.6	13.1	1.7	.06	.16	5.3	3
TREES REMAINING PARTLY OVERTOPPED SINCE CUTTING							
1.0	6.5	2.7	77.1	.04	.17	2.0	8
2.1	7.1	3.7	23.9	.04	.18	3.2	11
3.0	7.5	4.4	11.7	.04	.17	2.7	9
4.0	9.0	5.7	8.8	.04	.18	2.5	13
4.8	8.8	6.0	5.2	.03	.14	2.0	8
5.7	9.8	6.7	4.5	.03	.14	2.0	3
6.6	11.5	7.7	4.8	.03	.18	1.0	2
TREES REMAINING OVERTOPPED SINCE CUTTING							
1.1	5.3	2.3	45.0	.03	.17	4.9	9
2.1	5.2	3.2	10.7	.03	.14	5.7	14
3.1	6.4	4.1	7.0	.03	.13	3.7	21
4.0	7.0	4.7	4.7	.02	.13	3.0	6
5.0	7.9	6.1	3.0	.03	.13	4.3	10
6.2	9.1	7.2	2.3	.03	.13	1.0	1

[1]Outside bark at breast height (4½ feet above ground level.)

TABLE 4. Diameter growth of red spruce and hemlock after removal of largest trees 17 years before measurement (Turkey Run, Tucker County, W. Va.)

Average diameter[1] at time of cutting	Average diameter[1] 17 years after cutting	Average diameter[1] 17 years after cutting if original growth rate had continued	Increase in rate of average annual growth in basal area as result of cutting	Average annual diameter growth		Average time elapsing before increased growth began	Basis
				For decade before increased growth began	During period of increased growth		
Inches	*Inches*	*Inches*	*Percent*	*Inches*	*Inches*	*Years*	*No. of trees*
RELEASED SPRUCE REMAINING FREE SINCE CUTTING							
1.1	3.5	2.7	22.7	0.03	0.16	8.0	1
1.9	4.0	2.6	14.0	.03	.14	6.2	6
3.1	5.8	4.2	9.9	.05	.17	4.7	13
4.2	6.1	4.8	4.6	.04	.18	8.5	11
4.9	7.0	5.6	4.3	.03	.17	6.1	8
6.0	7.8	6.6	2.8	.04	.15	6.5	13
7.1	9.3	8.0	2.8	.05	.15	4.7	7
8.1	10.0	8.7	2.0	.04	.14	6.2	6
9.0	11.6	10.4	2.0	.03	.19	6.4	7
10.0	11.7	10.7	1.3	.04	.15	6.8	4
14.3	15.5	15.2	1.2	.04	.10	0.0	1
SPRUCE REMAINING PARTLY OVERTOPPED SINCE CUTTING							
1.0	3.0	1.8	19.0	.04	.14	6.9	7
2.0	4.1	2.5	15.2	.02	.15	5.8	4
3.0	4.1	3.4	3.4	.03	.11	9.5	4
4.2	6.2	4.7	5.6	.04	.21	8.5	4
5.1	6.0	5.6	1.0	.03	.11	11.2	4
7.4	8.8	7.5	2.3	.01	.08	0.0	1
SPRUCE REMAINING OVERTOPPED SINCE CUTTING							
1.1	3.2	1.8	30.2	.04	.14	5.7	3
2.1	3.8	2.4	12.3	.02	.10	4.3	12
3.0	5.0	3.5	7.8	.03	.12	3.5	4
4.0	4.8	4.3	1.7	.02	.09	10.0	1
5.5	6.2	5.9	0.7	.02	.08	9.0	1
RELEASED HEMLOCK REMAINING FREE SINCE CUTTING							
1.0	5.6	2.6	132.4	.03	.29	3.5	2
2.0	6.0	3.4	32.4	.07	.18	4.0	2
3.5	8.3	4.6	22.9	.06	.30	4.0	1
5.2	8.6	7.0	5.6	.08	.21	6.0	2
6.3	9.1	7.2	4.8	.04	.20	5.5	2
7.0	11.4	7.4	9.0	.02	.34	5.0	1
7.9	12.6	9.3	6.8	.08	.31	5.2	4
9.0	13.2	11.1	3.7	.11	.30	6.0	3
10.1	13.3	11.1	3.1	.05	.18	4.7	3
10.8	14.6	12.4	3.0	.10	.23	2.5	2
11.7	15.4	13.4	2.4	.09	.27	6.0	4
13.2	16.2	15.0	1.3	.10	.18	5.0	1
15.0	19.2	16.6	2.4	.10	.30	6.5	2
16.8	20.2	20.0	.2	.17	.18	7.0	1

[1]Outside bark at breast height (4½ feet above ground level.)

For released trees remaining free for 35 years after cutting the average annual increase in rate of basal area growth varied from 141.8 percent in 1-inch trees, to 1.7 percent in 11-inch trees (table 3). The increase in basal area growth rate for trees which continued to be overtopped was much less, varying from 45 percent in 1-inch trees to 2.3 percent in 6-inch trees. The increase since cutting in growth rate of free and overtopped trees is more clearly shown for the various diameter classes in figures 9 and 10. Figure 11 shows the increase in average diameter for all spruce trees measured on the areas logged 35 years prior to the study.

The increased growth of released red spruce and eastern hemlock remaining free after a cutting 17 years prior to examination is shown in table 4. The area studied in this case is in the lower portion of the spruce type, where the spruce is growing more slowly than that in the upper portion of the type (table 3). The hemlock on this area is growing much more rapidly than the spruce. Comparing the growth of spruce in West Virginia with that of the spruce in the Adirondacks, the West Virginia spruce apparently responds, after cutting, with a greater increase in growth rate, perhaps because of the larger proportion of hardwoods in the Adirondack forest and the more rapid closure of their crowns (McCarthy, 1919; Pinchot, 1898).

It is to be expected that in stands comparable as to site and composition, the degree of increase in growth rate of individual trees after cutting will depend upon the proportion of the stand removed. But where the cutting is uniformly heavy, as evidently was the case in the examples cited, differences in the increase of growth must be due to other factors. An important influence, emphasized more strongly by the present study than even the degree of cutting, is crown development.

Growth data obtained in the present study show that while the individual trees seldom failed to increase their growth rate when given more light and soil moisture by the removal of trees close to them, the time at which this increased growth began varied from 1 to 11 years (1 to 6 years on the better sites and 3 to 11 years on the poorer). The magnitude of this lag, as well as the amount of the increased growth for trees of the same size on a given site, depends quite largely upon crown development. Trees with large, well-formed crowns and dense foliage respond more promptly and reach a higher growth rate under the stimulus of increased growing space than trees with small, poorly formed crowns and thin foliage. The maximum rate is generally attained within 10 to 15 years after cutting, depending on the rate at which the released trees develop crowns sufficiently large and full to support the highest growth rate. The increase is discernible for many years, depending not only on the rate of crown development in the released trees, but also on the invasion of hardwoods and the rate of closure of the crown canopy.

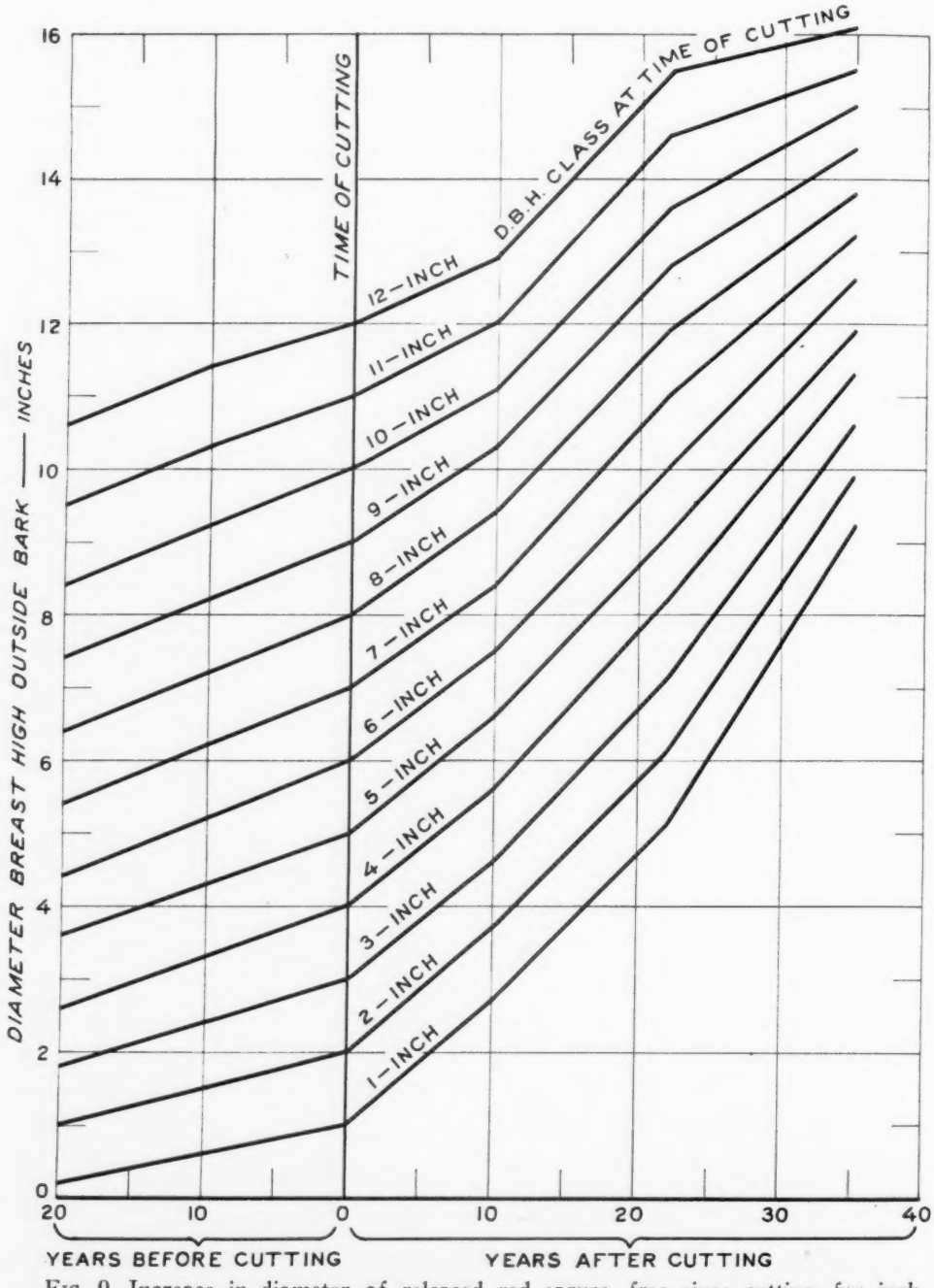


FIG. 9. Increase in diameter of released red spruce, free since cutting, for inch classes. Based on analysis of 381 trees, 22 and 35 years after cutting. Cheat River watershed, Pocahontas and Randolph Counties, West Virginia.

Overtopped trees growing slowly at time of cutting show a much greater response to release than those which always had their crowns free or in the upper part of the overstory, although the rate of growth attained may be

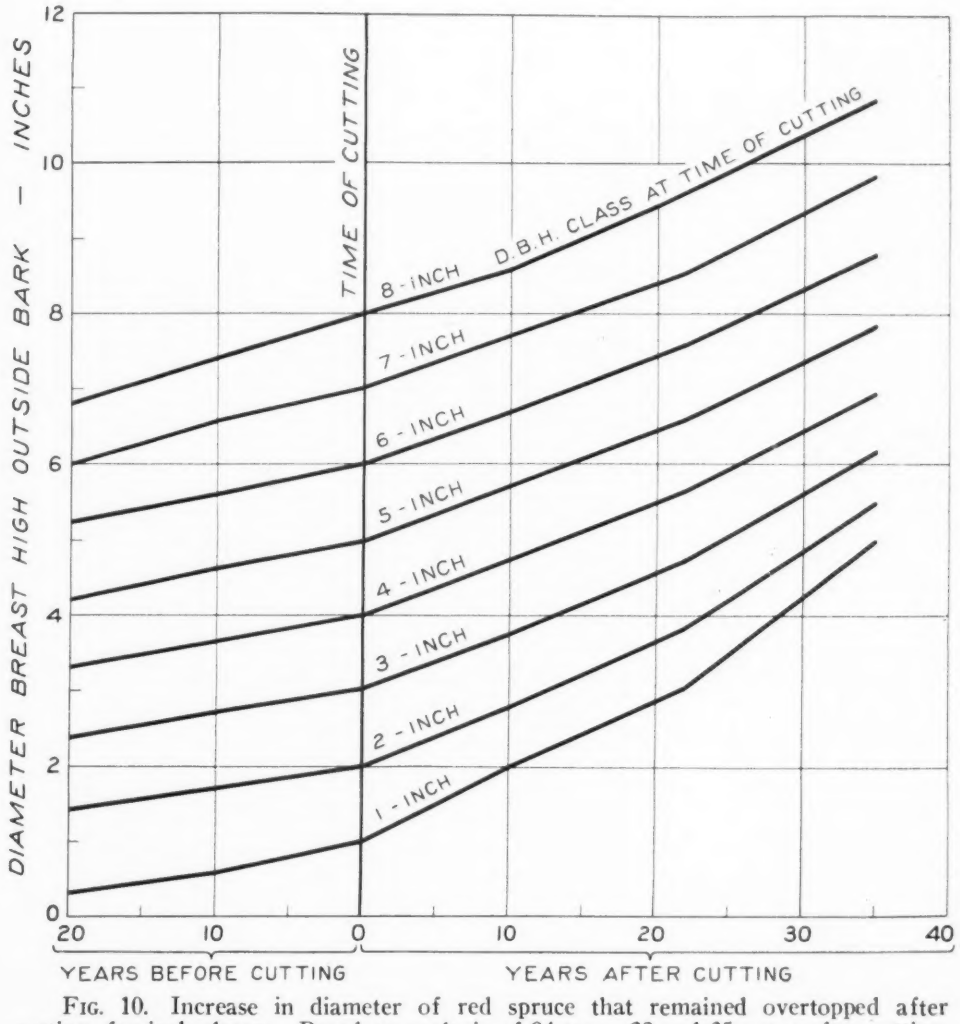
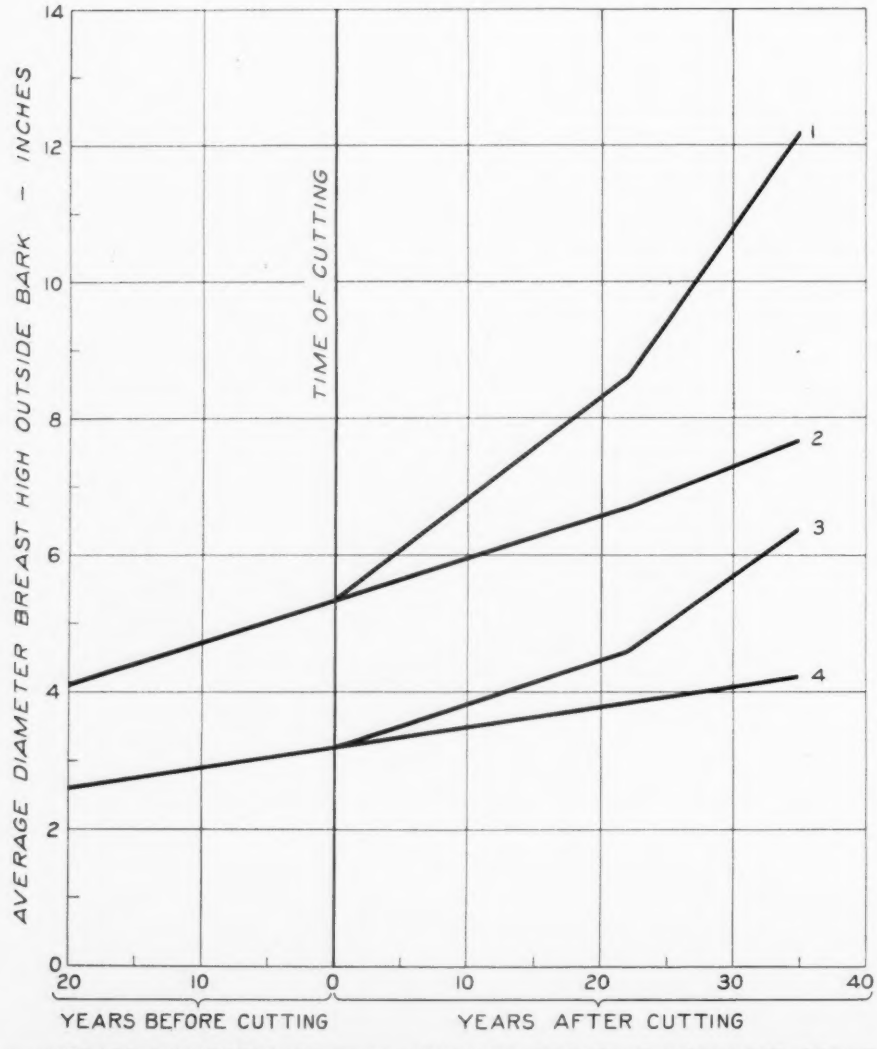


FIG. 10. Increase in diameter of red spruce that remained overtopped after cutting, for inch classes. Based on analysis of 94 trees, 22 and 35 years after cutting. Cheat River watershed, Pocahontas and Randolph Counties, West Virginia.

much less. As the trees become larger the percentage of increase, as well as the absolute growth after cutting, falls off until it is almost negligible in the larger trees (tables 3 and 4). It is also made evident by this study that to obtain the maximum increase in growth rate it is necessary to select the trees carefully and leave them well distributed and not too close to each other. The crown provides the most reliable index of what may be expected from the trees remaining after cutting. A long, dense, pointed crown generally indicates a thrifty, rapidly growing tree. Observations showed that crown length and form of top are most significant. Trees with long, pointed crowns, even though narrow, were usually growing more rapidly than the average trees of the same size.



1. AVERAGE DIAMETERS OF FREE-CROWNED TREES AT INCREASED GROWTH RATE; 2. AVERAGE DIAMETERS THAT FREE-CROWNED TREES WOULD NOW HAVE IF THEY HAD CONTINUED TO GROW AT THE CURRENT RATE AT TIME OF CUTTING. 3. AVERAGE DIAMETERS OF OVERTOPPED TREES AT INCREASED GROWTH RATE; 4. AVERAGE DIAMETERS THAT OVERTOPPED TREES WOULD NOW HAVE IF THEY HAD CONTINUED TO GROW AT THE CURRENT RATE AT TIME OF CUTTING.

FIG. 11. Increase in average diameter of free-crowned and overtopped red spruce following cutting. Based on analysis of 381 free-crowned and 94 overtopped trees, 22 and 35 years after cutting. Cheat River watershed, Pocahontas and Randolph Counties, West Virginia.

CONDITIONS ON BURNED CUT-OVER LANDS

The depletion of the Southern Appalachian spruce forest is due chiefly to fire following destructive logging. Practically all the cut-over spruce lands have been burned one or more times. The common result has been the utter destruction not only of the forest, but even of the organic matter in the surface soil on which it grew.

IMMEDIATE EFFECTS OF FIRE

Although the fire hazard in the natural spruce forest is extremely low, heavy cutting leaves a large amount of slash, which on drying out becomes highly inflammable, creating a hazard so great that almost invariably logging is followed by fire. Such a fire is generally hot enough to kill all live trees not protected by surface moisture, and often leaves large quantities of unconsumed wood to provide abundant fuel for a subsequent fire (fig. 12). A burned area becomes a hazard again as soon as the crop of vegetation following the first fire has created a cover of dry litter sufficient to carry fire over the surface to the dead wood. Ordinarily, however, a slash fire destroys not only the timber, the advance reproduction, and the logging slash left by the cutting, but also the organic matter and the microorganisms of the upper soil layer.

This destruction of the forest floor as well as the slash exposes the remaining soil to erosion. Beating rains, common in the higher mountains, carry off the soil both by widespread sheet erosion and by local gullying (fig. 13) until at last the underlying rock is exposed. The amount of material removed by erosion and carried off by the streams is thus increased enormously (Korstian, 1929). Site deterioration through loss of the surface soil is particularly rapid in the spruce belt, during the first few years after each successive fire.

FIG. 12. This area has not restocked naturally to conifers in 20 years following cutting and fire. Within 2 years after the last fire blackberry briers, pin cherry, and yellow birch usually spring up on cut-over and burned spruce lands.

With the cessation of fires and the reestablishment of a vegetative cover, this destructive process gives way to one of progressive development, involving not only the vegetation but the site itself. As the run-off is checked, erosion is reduced, and organic matter is added to the remaining soil, improving its structure and fertility. Thus the productive capacity of the site is proportionately increased, until at last its original productivity becomes restored; but this process is very slow on badly depleted areas.

HARDWOODS FOLLOW FIRES ON CUT-OVER SPRUCE LANDS

When fires follow logging on spruce lands, they generally destroy all the conifers left standing except occasional trees along streams or in unusually moist places. Where the slopes are not too steep and erosion and gullying too rapid, a surprising increase occurs in the number of hardwoods, especially yellow birch and pin cherry. Table 5 illustrates this characteristic result on areas from North Carolina to West Virginia that had been logged 5 to 20 years earlier and burned shortly afterwards.

The vegetation appearing within a year after the fire is frequently a dense, rank growth of blackberry and raspberry briers, and is promptly followed by an abundance of pin cherry and yellow birch (fig. 14). This cover is mostly of sprout origin, particularly on areas which were burned several years after cutting so that hardwoods had already had a chance to seed in.

FIG. 13. Serious erosion advances rapidly following heavy cutting on spruce lands, as shown by the condition of this skid road within a year after logging.

FIG. 14. Ten years after the fire hardwoods still predominate although they are growing slowly and spruce seedlings are gaining a foothold on the thin rocky soil.

The cherry, because of its rapid early growth, usually gains a dominant position in the new stand, holding it for 15 to 20 years. Then it dies out and is commonly replaced by yellow birch and other less predominant hardwoods. Tall shrubs, such as rhododendron, mountain laurel, serviceberry, and huckleberry, contribute to the great density of the young stand, although as a rule they occupy subordinate positions.

A second fire generally kills any spruce and fir that may have escaped the earlier one, resulting in the almost complete annihilation of the conifers and the prompt establishment of a hardwood cover (table 6). The second example in table 5 is representative of an area of several thousand acres in the Black Mountains, Yancey County, N. C., which 8 or 10 years before the examination had been severely burned on two occasions after logging. It furnishes an illustration of the replacement of conifers by hardwoods after two fires on cut-over spruce lands, even though they are below the mountain tops on which occur uncut spruce-fir forests capable of producing seed (fig. 3). Four acres of strip tallied on this burn showed an average conifer stand per acre of only 190 red spruce seedlings, having a mean height of 1 foot, and 126 southern balsam firs averaging 3 feet in height. The same area supported an average of 804 yellow birch, 1,602 pin cherry, 80 mountain ash, 9 willow, and 6 mountain maple saplings per acre, all of them under 5 inches in diameter. No larger living trees of any species were found

TABLE 5. Composition (number of trees per acre) of present stand on burned cut-over spruce lands.

Period since cutting and species in present stand[1]	Diameter breast high (inches)			
	Less than 1	1 – 4	5 – 12	More than 12
Cut-over 5 years:[2]				
Red spruce	19	1	0	0
Southern balsam fir	6	2	0	0
Eastern hemlock	6	0	0	0
Commercial hardwoods (yellow birch)	6,985	1	1	3
Small trees and tall shrubs (pin cherry, mountain maple, rhododendron)	20,833	552	1	0
Cut-over 8 to 10 years:[3]				
Red spruce	190	0	0	0
Southern balsam fir	126	6	0	0
Eastern hemlock	2	0	0	0
Commercial hardwoods (yellow birch)	786	18	0	0
Small trees and tall shrubs (pin cherry, mountain ash, willow, mountain maple)	787	910	0	0
Cut-over 11 years:[4]				
Red spruce	58	0	1	0
Eastern hemlock	3	0	0	0
Commercial hardwoods (yellow birch)	18,490	269	2	1
Small trees and tall shrubs (pin cherry, mountain maple)	1,540	1,109	1	0
Cut-over 13 years:[5]				
Red spruce	18	11	1	0
Southern balsam fir	10	13	1	0
Eastern hemlock	2	0	0	0
Commercial hardwoods (yellow birch)	1,950	113	1	2
Small trees and tall shrubs (pin cherry, rhododendron)	21,995	1,808	1	0
Cut-over 12 to 13 years:[6]				
Red spruce	82	11	0	0
Eastern hemlock	94	6	0	0
Commercial hardwoods (yellow birch, red maple, black cherry, sugar maple, sweet birch, beech)	...	1,205	2	0
Small trees and tall shrubs (pin cherry, mountain holly, striped maple, serviceberry)	...	648	2	0
Cut-over 20 years:[7]				
Red spruce	215	69	2	0
Commercial hardwoods (yellow birch, beech)	0	2,101	65	0
Small trees and tall shrubs (pin cherry, mountain holly, serviceberry, striped maple, mountain maple)	0	380	47	0

[1]Species in parentheses following "Commercial hardwoods" and "Small trees and tall shrubs" constitute approximately 90 percent of these groups.
[2]Burned within a year after cutting. Based on 3.5 acres of strip tally on Pigeon River watershed, Haywood County, N. C.
[3]Burned twice within 2 years after cutting. Based on 4.0 acres of strip tally on Black Mountains, Yancey County, N. C.
[4]Burned within a year after cutting. Based on 1.8 acres of strip tally on Unaka Mountain, Unicoi County, Tenn.
[5]Burned within a year after cutting. Based on 4.2 acres of strip tally on Plott Balsam Mountains, Haywood and Jackson Counties, N. C.
[6]Burned 5 years after cutting. Based on 2.6 acres of strip tally on Otter Creek watershed, Randolph County, W. Va.
[7]Burned within a year after cutting. Based on 3.1 acres of strip tally on Shavers Fork of Cheat River, Randolph and Pocahontas Counties, W. Va.

on the burn. Practically all the hardwoods had already overtopped the spruce and fir.

Ordinarily slash fires on cut-over spruce lands are so hot, and the litter of the forest floor is so completely destroyed, that the possibility of repro-

TABLE 6. Composition (number of trees per acre) of present stand on lands burned twice after logging (Shavers and Cheat Mountains, Randolph and Pocahontas Counties, W. Va.)

Period since cutting and species	Diameter breast high (inches)			
	Less than 1	1 – 4	5 – 12	More than 12
Cut and burned 18 years and burned again 7 years before examination:[1]				
Red spruce	8	0	0	0
Eastern hemlock	5	0	0	0
Commercial hardwoods[2]	.....	1,093	21	0
Small trees and tall shrubs[3]	.....	1,107	10	0
Cut and burned 13 years and burned again 1 year before examination:[4]				
Commercial hardwoods[5]	396	2	0	0
Small trees and tall shrubs[6]	3,564	126	0	0

[1]Based on 1.7 acres of strip tally.
[2]Sweet birch 32.6 percent, beech 23.9 percent, yellow birch 18.3 percent, mountain magnolia 11.3 percent, and red maple, cucumber, sugar maple, chestnut, yellow poplar, black cherry, red oak, and white ash made up the remainder.
[3]Pin cherry 46.2 percent, aralia 34.0 percent, witch hazel 6.4 percent, sumac 5.8 percent, and serviceberry, mountain holly, striped maple, mountain ash, mountain maple, and largetooth aspen made up the remainder.
[4]Based on 0.5 acre of strip tally; the stump tally showed that an average of 101 red spruce and 30 balsam fir over 4 inches in diameter were removed per acre in logging.
[5]Red oak 67 percent and yellow birch 33 percent.
[6]Pin cherry 79.9 percent, mountain holly 20.0 percent, and serviceberry made up the remainder.

duction springing from seed accumulated in the litter is slight indeed. And if the burned area is large, the restoration of the original coniferous type of forest will be extremely slow (figs. 15 and 16).

In order to learn whether the quantity of conifer reproduction on twice-burned spruce land bears any relation to the distance from the source of seed, a tally was made in the Black Mountains, along lines running down the slopes away from the strip of living timber on the main crest. Instead of the regular decrease in number of seedlings that might have been expected, proportional to the distance from the uncut stand, the reproduction was found very irregularly distributed (table 7). This is attributable to the variation in strength and movement of wind, to the great width of the zone within which seed is distributed down slope by winds, and to the variability of seed-bed conditions. More conifer reproduction was found in moist situations under pin cherry than elsewhere. For example, the abundant spruce reproduction illustrated by chains 24 to 36, on strip 3, was under pin cherry. On the other hand, a dense growth of shallow-rooted raspberry and blackberry briers apparently caused so much root competition for soil moisture as to result in the establishment of very few spruce and balsam seedlings (chains 4 to 22 on strip 3 and most of strip 5).

Reproduction more proportionate in quantity to the distance from the source of seed was found on an area severely burned following cutting. This area was located on the broad and relatively flat top of Shaver's Mountain, Randolph County, W. Va. Here the strip tallies were run from a stand of mature red spruce and eastern hemlock into the adjacent burn (table 8).

FIG. 15. A slowly growing stand of hardwoods, chiefly yellow birch, under which young spruce has become established on thin rocky soil, 20 years after a fire. Here many of the spruce saplings may be expected eventually to gain a dominant position in the crown cover. West Virginia.

Groups of conifer seedlings dense enough to form a satisfactory stand were usually found within 7 chains of the mature timber, and scattered seedlings were found up to 33 chains distant. Unfortunately all of the conifer seedlings were overtopped by a much denser stand of hardwoods, which would confine them to the understory until such time as the hardwood cover is opened by cutting or some other disturbance. Hardwood stands beyond the present seeding range of the conifers will probably remain for several generations before they are gradually replaced by the original conifer cover.

FIG. 16. The original spruce forest has been completely replaced 20 years after burning by a hardwood stand in which sweet and yellow birches predominate. Due to the better soil conditions the hardwoods have developed rapidly and there is no prospect of the spruce reestablishing itself within the next generation. West Virginia.

MEASURES NECESSARY TO RESTORE CONIFER FORESTS IN THE SPRUCE TYPE

PROTECTION FROM FIRE

There is no prospect of growing successive crops of spruce timber where fires continue to occur. The principal condition predisposing to fire on logged spruce lands is the presence of slash. Slash fires may get beyond the control of one man in a few minutes, and most fires do so within 30 minutes of their start, if fuel conditions are favorable. For that reason a speed of attack commensurate with the hazard and risk which obtain in the spruce type is necessary if fires are to be reached while still susceptible of being controlled. In fact, the greatest fire risk known to exist anywhere in the Southern Appalachian region is found on heavily cut or clear-cut spruce lands, where the slash is too heavy to permit any practical method of disposal. Here nothing but unremitting care will prevent devastating fires.

Forest fires are most frequent in the spring, after the winter rains have ceased and before the vegetation has advanced far enough to keep the ground cover from drying out, and in the autumn, after the leaves have fallen. Fires are rare during the season of active growth and cease entirely with the fall of snow; but heavy slash creates a fire hazard even in dry periods of

TABLE 7. Number of seedlings per acre found on five strips 8 to 10 years after mature timber had been cut and the areas burned over twice within the next year (Black Mountains, Yancey County, N. C.)

Distance from green timber (chains)	Strip 1		Strip 2[1]		Strip 3[1]		Strip 4[1]		Strip 5	
	Red spruce	Southern balsam fir	Red spruce	Southern balsam fir	Red spruce	Southern balsam fir	Red spruce	Southern balsam fir	Red spruce	Southern balsam fir
1	66	33	...	...	...	...	...	...	...	...
2	0	132	214	825	143	314	1,386	116	0	33
3	33	99	...	...	...	...	...	...	...	..
4	165	0	33	66	0	0	132	33	0	99
5	132	33	...	...	...	...	...	...	...	..
6	198	0	66	544	0	0	528	165	0	0
7	132	0	...	...	...	...	...	...	..	..
8	33	0	198	1,386	0	0	1,040	165	0	0
9–10	33	0	0	99	0	0	...	...	0	0
11–12	99	0	0	0	0	0	...	...	0	0
13–14	0	0	0	0	99	16	...	...	0	0
15–16	0	0	0	0	50	16	...	...	0	0
17–18	0	0	0	16	0	0	...	...	0	0
19–20	0	0	0	0	0	0	...	...	33	0
21–22	0	0	0	0	66	0	...	...	0	0
23–24	66	0	0	0	346	16	...	...	0	0
25–26	33	0	...	...	396	16	...	...	0	0
27–28	0	0	...	...	99	0	...	...	0	0
29–30	0	0	...	...	248	16	...	...	0	0
31–32	0	0	...	...	656	16	...	...	0	0
33–34	0	0	...	...	198	0	...	...	0	0
35–36	...	...	...	...	165	0	...	...	...	..

[1]Eastern hemlock was found on the sixth chain of strip 2 and on the thirtieth chain of strip 3 at the rate of 16 per acre, and on the second chain of strip 4 at the rate of 33 per acre.

brief duration, and during very dry winters fires may occur even in January. In the southern part of the Appalachian region the active season of spring fires comes generally between the middle of March and the middle of May. The autumn season lasts about 8 weeks beginning the middle of October. Farther north the fire season begins and closes earlier in the fall and does not last so long in the spring.

During these seasons the fire hazard is so great that the maintenance of an adequate organization for the prompt detection and suppression of fires is absolutely necessary. Wherever Federal, State, or other public agencies for fire prevention exist, these should cooperate with and supplement available private organizations in providing the intensive protection required for cut-over spruce lands.

FOREST PLANTING TO REPLACE SPRUCE

Planting will undoubtedly be necessary if the original coniferous cover on cut-over and severely burned spruce-fir lands is to be restored within a reasonable time (fig. 12). The best time for planting is immediately after a fire. Not only will the cost be less, but the early competition from native vegetation will be at a minimum. But planting should be undertaken only on lands which are assured of adequate protection against fire.

TABLE 8. Number of seedlings per acre found on four strips 8 years after mature timber had been cut and the areas burned over within the next year (Shaver's Mountain, Randolph County, W. Va.)

Distance from green timber (chains)	Strip 1		Strip 2		Strip 3		Strip 4	
	Red spruce	Eastern hemlock	Red spruce	Eastern hemlock	Red spruce	Eastern hemlock	Red spruce	Eastern hemlock
1	1,254	858	2,244	462	858	792	594	1,023
2	1,584	462	1,452	297	363	165	231	495
3	1,980	297	660	66	693	528	495	462
4	1,650	99	858	330	693	132	462	462
5	1,056	132	231	99	561	462	693	462
6	396	330	297	66	165	132	297	1,188
7	462	198	66	66	396	99	132	924
8	165	0	363	33	264	66	99	198
9	33	0	66	0	165	33		
10	0	0	66	99	33	99		
11	0	0	99	132	66	33		
12	33	0	99	198	0	66		
13	99	0	66	132				
14	296	66	33	66				
15	33	0	33	132				
16	132	66	33	66				
17	132	0	0	198				
18	66	66	66	165				
19	66	33	99	0				
20	0	33	33	165				
21–22	66	66	165	33				
23–24	33	0	66	0				
25–26	0	33	0	99				
27–28	0	0	33	66				
29–30	33	33	0	99				
31–33	0	33	66	0				

Thrifty transplants of native red spruce and southern balsam fir provide the best stock for planting, especially those grown two years in the seed bed and one in the transplant bed. An additional assurance of success is offered by stock grown locally from seed collected in the vicinity or from nearby localities having similar climatic conditions.

A number of planting tests to determine the species most suitable for artificial restocking of cut-over and burned spruce lands have been conducted by the Appalachian Forest Experiment Station in the Black Mountains of North Carolina. Three separate plantings of red spruce resulted in 60 to 85 percent of the trees surviving at the end of the fifth year. The trees then averaged from 1.2 to 1.8 feet in height, and were growing vigorously. Other plantings of red spruce resulted in survivals of 88 percent at the end of the third year and 81 percent at the end of the fourth. One plantation showed a survival of 61 percent 11 years after planting, and the trees averaged 5.0 feet in height. During the first few years after planting the growth of spruce is always slow, but thereafter it may be expected to become more rapid.

Southern balsam fir has shown even better results. Five-year old plantations had 82 to 85 percent of trees surviving, with an average height of 1.5 to

1.8 feet. One fir plantation at the end of 11 years showed 80 percent of the trees surviving, an average height of 8.2 feet, and an average growth for the eleventh year of 1.84 feet.

Pitch pine *(Pinus rigida)*, which is not native to the spruce belt, has shown comparable survival—64 and 78 percent at the end of the sixth year—and good height growth—7.4 feet in 12 years—yet its future development on these sites remains a matter of conjecture. Because at lower altitudes it is able to grow on dry, exposed situations, it may in the end prove useful for planting poor sites at the higher elevations of the spruce type.

Norway spruce *(Picea excelsa)*, another species not native to the region, gave encouraging results 12 years after planting. One plantation had a survival of 74 percent, the trees averaging 6.8 feet tall and showing a current growth in height of 1.6 feet per year. In spite of this rapid early growth, the planting of Norway spruce must be regarded as experimental until it has shown its capacity to attain satisfactory size, form, and quality at maturity under the conditions where it is being tried out.

A number of other species exotic to the region have been tried experimentally. These include Norway pine *(Pinus resinosa)*, Scotch pine *(Pinus sylvestris)*, Japanese red pine *(Pinus densiflora)*, Japanese black pine *(Pinus thunbergii)*, lodgepole pine *(Pinus contorta)*, western white pine *(Pinus monticola)*, white spruce *(Picea glauca)*, white fir *(Abies concolor)*, European silver fir *(Abies pectinata)*, Douglas fir *(Pseudotsuga taxifolia)*, northern white cedar *(Thuja occidentalis)*, Japanese larch *(Larix leptolepis)*, and European larch *(Larix europaea)*. Several of these species have already failed, others are showing their unsuitability, and none have as yet demonstrated any superiority over the native red spruce and southern balsam fir for reforesting the devastated spruce lands in the Southern Appalachian Mountains.

The planting of seed in prepared seed spots has proved successful in one instance only—in West Virginia, where European larch attained a height of 20 to 30 feet in 15 years, and Norway spruce reached a height of 6 feet within the same period (fig. 17). Until long and thorough trials have demonstrated the superiority of introduced species over the native red spruce and southern balsam fir, these latter species alone should be used in plantations not established for purely experimental purposes.

Unless coniferous stands are especially desired, planting is not advocated for areas on which hardwoods of suitable form and development have already appeared or which they are likely to invade. The interfering trees would have to be cut back one or more times to release the planted conifers and the cost of the plantation would be correspondingly increased. Experimental plantings made under a cover of yellow birch and pin cherry resulted within a few years in poor survival and growth. Moreover it is reasonable to conclude, from the behavior of natural reproduction of conifers under a

FIG. 17. Cut and burned spruce lands not restocking with either conifers or hardwoods must be reforested artificially. Stand resulting from artificial seeding 15 years before with European larch and Norway spruce immediately following a fire.

hardwood cover, that as the stand of young hardwoods develops and becomes denser the growth rate of the red spruce and southern balsam fir will be reduced still further. They will remain in a suppressed, stunted condition, at least until the density of the overhead cover is reduced materially.

MANAGEMENT OF SPRUCE FOREST TO INSURE ITS PERPETUATION

If the spruce forest of the Southern Appalachians is to be perpetuated it must be managed very judiciously. The outstanding conclusion of the study is that clear cutting—the common practice of the past—is the most undesirable system that could be used because of the extent to which fire subsequent to cutting is likely to destroy the young growth and the soil. Even if fires do not follow, clear cutting causes drying out of the soil and litter, and thus reduces the chances for conifer reproduction. The best means of avoiding conditions favorable to devastating fires and serious erosion and of preserving adequate moisture for the establishment of spruce and fir seedlings is found in the method of selective, or partial, cutting. The virgin spruce forest, which is commonly made up of trees varying considerably in size and age, is especially well adapted to perpetuation by this method of cutting. Under this form of management only a portion of the trees—the larger mature individuals and such smaller ones as are injured in felling the large trees—are cut, leaving uncut a considerable portion of the stand. The growth of this residual stand provides the volume for similar cuttings periodically in the future.

The ideal result of a long series of selective cuttings should be a forest that can be opened up evenly and regularly, with a uniformly distributed crown cover amounting perhaps to 60 or 70 percent of the original, and with no large vacant spaces. This ideal cannot be achieved quickly except on small areas, because the distribution of tree sizes in the virgin forest is irregular. Where most or all of the trees in a group are large and overmature, the necessary harvesting will leave a wide opening. On the other hand, where the large trees are scattered among smaller ones, their removal will leave the forest in a condition more nearly approximating the ideal.

Since the bulk of the wood volume of the virgin forest may be contained in a relatively few large trees, a selective cutting that removes only 20 percent of the crown cover will take a much larger percentage of the total volume. The removal of the scattered large trees increases the light received by the crowns of their smaller neighbors, which respond with increased growth. Reproduction becomes established in the openings (fig. 18). The result of a well-executed series of partial cuttings should be the conversion of a more or less static forest into an active, producing forest, capable of maintaining satisfactory forest and watershed conditions and of supplying regular yields of commercial timber, approximately equal in volume to the growth between cuttings.

Partial cutting greatly lessens the fire hazard. In contrast to the very high hazard on clear-cut areas, very little danger from fire results from partial cuttings that leave as much as 50 to 75 percent of the original crown cover, because the forest floor is kept in a moist condition, favoring rapid

FIG. 18. Good reproduction of red spruce in small opening in stand such as results from partial or selective cutting.

decomposition of slash. If in addition the tops of felled trees are cut up and utilized for pulpwood, the slash menace will be still further reduced.

The volume and kind of trees to be removed in the first cutting will depend upon the distribution of size classes, the density of the stand, the species associated with the spruce, and other conditions. Stands containing much advance growth of red spruce and southern balsam fir, many of which are found in the upper part of the spruce belt, may be cut somewhat more heavily than stands in which advance growth is scarce or absent. The advance growth will shade the soil in the openings left by cutting and largely prevent the encroachment of hardwoods. Scattered merchantable hardwoods should be removed at the first cut (fig. 19), but where abundant or where their removal would unduly expose the conifers to windthrow (fig. 20), some should be left for a later cut. Moderate shade should be retained, admitting enough light for the development of spruce and balsam but not enough for the less shade-tolerant hardwoods, especially pin cherry and yellow birch. Broken, diseased, insect-infested, or poorly formed trees should be felled or girdled.

The great importance of advance growth of conifers as a basis for the new stand cannot be too strongly emphasized. Where abundant reproduction is found in the forest it is almost always advance growth, supplemented to some extent by seedlings germinating from seed produced just before cutting. As a general rule too many young spruces and firs, too small to have commercial value, are unnecessarily destroyed in logging. With ordinary precaution

FIG. 19. Mixed stand of hardwoods and spruce on deep, rich, well-drained soil 30 years after the merchantable red spruce and the best black cherry had been culled from it. More of the hardwoods, such as the large yellow birch in the center, should have been removed then. All merchantable hardwoods on this area are being cut along with the larger spruce.

FIG. 20. Shallow-rooted red spruce windthrown after the surrounding stand had been opened by heavy cutting.

in felling the larger trees much of this young growth can be saved without additional cost. The more of these trees that are saved in logging the more advanced will be the new stand on the cut-over land and the sooner it can be logged again. Obviously selective cutting is well suited to pulpwood logging by animals and flumes.

Cutting to a diameter limit, practiced occasionally in pulpwood logging of spruce and fir, may be regarded as a modification of selective cutting by which a yield sufficient to make the operation profitable is obtained periodically. Naturally the volume of material removed at each cutting as well as the intervals between successive cuts must vary with the diameter limit used. A fixed limit rigidly applied may to a large extent defeat the purposes of selective cutting, partly by leaving poor trees below the limit, and partly by taking good trees above the limit that are needed to fill thin places in the stand. The largest trees should be cut, of course, since their rate of growth is too slow to warrant their retention in the residual stand. On the other hand, it is wise to leave occasional vigorous, well-formed trees above the diameter limit, both to insure a more uniform spacing and to obtain a material increase in their value. In partial cuttings where spruce pulpwood is one of the products, trees as small as 5 inches in diameter may be merchantable, and it may be desirable from both the silvicultural and the economic points of view to cut

trees of that size at certain places in the stand, even though the general diameter limit is fixed at 10 or 12 inches. Advantage should be taken of the operation to remove dead trees and snags so as to reduce the fire hazard. When properly employed, the diameter limit serves merely as a guide to make sure that the growing space is utilized by well-formed, rapidly growing trees.

Girdling is often a good way of eliminating old and defective hardwoods, and practical demonstrations have shown that it can be done at a cost which makes it applicable in the management of spruce stands (Cary, 1928; Churchill, 1927; Westveld, 1928). But it should be restricted to the release of well-established conifer reproduction, as otherwise it is probable that young hardwoods of seedling or sprout origin will spring up in the openings. Where a market can be developed for hardwoods, girdling them would not be desirable except in the case of trees showing poor form and quality. If they are girdled in stands containing a large number of shade-tolerant species, like beech and sugar maple, a subsequent removal of hardwood saplings may be required to free small spruce and fir from oppressive competition. As a rule girdling should not be employed until a few years after logging, when it is possible to decide with accuracy which trees constitute a menace to the advance growth.

Further study of the management of the Southern Appalachian spruce forest is needed before all questions can be answered with finality. Indications now point strongly to the desirability of always studying spruce stands before decision is made to cut in them. The values of the spruce forest for other purposes than timber often equal or exceed its value for timber. There are many cases where only small, carefully selected portions of a stand should be cut over and others where, in order to preserve satisfactory watershed and natural forest conditions, no cutting should be done. This is especially true on thin, rocky soils where clear cutting results in the destruction of watershed values and natural forest conditions and where partial cutting in poor stands might be overly expensive because of the small amount of timber that could be removed at any one time or where excessive windthrow might follow in the residual stand.

SUMMARY

1. The usefulness of the spruce forest of the Southern Appalachians, both for saw timber and pulpwood, has resulted in large-scale exploitation, followed generally by fire and leading to the virtual destruction of the type.

2. The urgency of preserving what is left of the spruce forest, and of restoring it, so far as possible, where it has been destroyed, prompted a study of virgin, cut-over and burned spruce lands to obtain information on: (1) The conditions prevailing on such lands; (2) the reproduction characteristics of spruce; (3) the obstacles to reproduction; and (4) the measures by which the spruce forest may be restored and perpetuated.

3. Of the several tree species found in the spruce forest, red spruce, the most valuable, is the most difficult to reproduce naturally. The greatest obstacle to natural reforestation is the drying out of the surface layer of moss and peat after clear cutting or its destruction by fire, followed by the surface drying of the mineral soil.

4. Due to the more rapid growth of its competitors, spruce is most abundant, not where the best conditions for its growth exist, but where its competitors are less able to grow. On the deeper, better drained soils the proportion of spruce and fir reproduction that comes in after heavy logging is reduced through the encroachment of aggressive hardwoods.

5. The increase in growth rate of the residual stand following cutting varies widely with the extent to which the trees have remained free since cutting and also with the size and condition of the trees at the time of release. Crown length and form of top provide the most reliable index of amount of increased growth following cutting. A long, dense, pointed crown generally indicates a thrifty, rapidly growing tree.

6. The depletion of the Southern Appalachian spruce forest is due chiefly to fire following destructive logging. Practically all the cut-over spruce lands have been burned one or more times. The common result has been the utter destruction not only of the forest, but even of the surface soil on which it grew. Destruction of the forest floor along with the slash exposes the remaining soil to erosion. When fires follow logging on spruce lands, they generally destroy all the conifers left standing except occasional trees along streams or in unusually moist places. Where the slopes are not too steep and erosion and gullying not too rapid, a surprising increase occurs in the number of hardwoods, especially yellow birch and pin cherry.

7. Forest and slash fires must be controlled if conifer forests are to be restored on cut-over and burned spruce lands. Forest planting will undoubtedly be necessary if the original conifer cover is to be restored on these lands within a reasonable time. The best time for planting is immediately after a fire, at which time not only will the cost be less but the early competition from native vegetation will be at a minimum. Planting should be undertaken only on lands which are assured of adequate protection from fire and where serious hardwood competition does not exist or can be eliminated through subsequent cleanings.

8. If the southern spruce forest is to be perpetuated it must be managed very judiciously. Where cutting is desirable, the method of selective, or partial, cutting is recommended as far superior to the clear cutting commonly followed in the past. It will doubtless be desirable to exclude any kind of cutting of live trees in certain areas of spruce forest the value of which is very high for the preservation of satisfactory watershed cover or natural forest conditions.

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